

PERCEPTUAL ENVIRONMENT AND DEVELOPMENT
OF CAT VISUAL SYSTEM

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OF CAT VISUAL SYSTEM

by

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SCOPE AND CONTENTS:

Kittens were raised with early visual input restricted to horizontal, vertical, or oblique (45°) lines to determine the oculomotor consequences of such early restriction, and the limits of early neural plasticity.

- (i) All animals developed pendular nystagmus (frequency 3-5 Hz) which appeared to be related to active visual search, and was lowest in amplitude for animals exposed to oblique lines.
- (ii) Many cats developed convergent squint which was most severe for those exposed to horizontal lines.
- (iii) Abnormal binocular functioning of visual cortical units was found in all restricted animals.
- (iv) The stimulus orientation of maximum response corresponded to the experienced orientation for most units encountered in the animals exposed to vertical or horizontal lines.
- (v) In animals exposed to oblique lines all stimulus orientations appeared to be represented in the cortex; units responding maximally to the experienced orientation were not most often encountered.

The results were discussed in terms of possible anatomical constraints on visual plasticity and a preliminary model of visual development was explored.

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Introduction

The process by which an animal is able to extract visual information from its environment remains essentially mysterious. The aim of the present study is to attempt to shed some light on this process by examining the structure of its development.

In this short review the role of early visual experience in structuring and maintaining the visual system will be considered, with special emphasis on information from the cat since this is the experimental animal used in the present study.

The effects of several types of early visual experience have been investigated. Animals have been raised in normal laboratory environments as well as under various conditions of deprivation and enrichment (for reviews see Pettigrew, 1972; Edds, Barkley, and Fambrough, 1972; Hubel, 1967). In general, it has been found that in young visually naive cats cortical cells can be found which are similar in many ways to those seen in the visual cortex of adult cats (Hubel & Wiesel, 1963; Barlow & Pettigrew, 1971). An important difference, however, is that stimulus requirements for maximum response are much less specific for kitten cortical cells than for cells in adult cortex. The coarser tuning of kitten cortex has been shown with regard to both stimulus orientation as well as image disparity between the two eyes (Pettigrew, 1972). Experiments on monocular and binocular deprivation in kittens (Hubel & Wiesel, 1963, 1965; Wiesel & Hubel, 1963, 1965) have shown that these procedures appear to be most effective in disturbing neural function during what has been called a critical period (3 weeks to 3 months in cats). In addition, these experiments have highlighted the importance of competitive interactions in neural

development by showing that the effects of monocular deprivation are more severe than the effects of binocular deprivation.

The importance of competition in visual development has been shown most elegantly in a series of studies by Guillery and his colleagues. Guillery and Stelzner (1970) found as did Wiesel & Hubel (1963) that in animals deprived of vision in one eye, cells in the dorsal lateral geniculate nucleus of the thalamus (LGNd) receiving input from the deprived eye failed to develop. Guillery and Stelzner found, however, that the failure of development of geniculate cells was restricted to the portion of the geniculate receiving binocular visual input. Thus, these authors hypothesized that failure of cell growth in the geniculate was due not only to the absence of visual input but also to the presence of competing input from the non-occluded eye. Guillery (1972) investigated this hypothesis by raising animals with one eye occluded and discrete retinal lesions in the non-occluded eye. The effect of the discrete lesion was to remove competitive input from a small portion of the deprived geniculate lamina corresponding to the damaged retinal area. Guillery found that the cells in the deprived lamina of these animals failed to develop, except for the region corresponding to the destroyed retina in the open eye. Thus, cells in the LGNd receiving input from one eye fail to develop if the eye is deprived of visual input and if input is present on corresponding regions of the other eye.

Recently, experimenters have sought to determine the effect of specific pattern input on cells in the developing visual system. Early input restricted to a single orientation (vertical or horizontal), either with respect to gravity (Blakemore & Cooper, 1970) or with respect to

the head (Hirsch & Spinelli, 1970) has been reported to cause the orientation specificities (Blakemore & Cooper) or the receptive field shape (Hirsch & Spinelli) of cortical neurons to shift in the direction of the exposed orientation. These altered orientation characteristics have been shown to be maintained even after periods of nearly two years in a normal laboratory environment (Spinelli et al., 1972). The experiment of Blakemore & Cooper has been reported to be replicated by Mize & Murphy (1973) although these same authors reported an inability to produce the effect in rabbits, underlining species differences in visual development. Recently, Blakemore and Mitchell (1973) have reported that as little as one hour of vertical visual experience on day 28 will produce an absence of neurons responding to stimuli at orientations greater than + or - 30 degrees from vertical.

The effects of specific pattern input on the characteristics of cortical neurons in the cat have been generally interpreted as indicating that the feline visual system, though highly organized at birth, depends on early input for the final structuring of visual connections. The mechanism of final structuring has been unspecified but workers in this area have assumed that a great degree of modification in visual connections is possible. The model of visual development implied in much of this work is that the visual system at birth is infinitely modifiable with respect to characteristics of cortical neurons; input during a critical developmental period will effectively mold the characteristics of cortical units in its image. This approach is apparent in the work of Hirsch & Spinelli who raised an animal exposed only to the pattern of a bullseye during early life. These authors report that the receptive fields of cells

encountered in the cortex of this animal were bullseye shaped. The view that the early visual system has unlimited plasticity is most articulately stated in two recent studies (Pettigrew & Freeman, 1973; Van Sluyters & Blakemore, 1973). Though different procedures were used, in both of these studies cats were raised with visual exposure limited to a pattern of dots. Both studies report that in the cortex of the dot raised cats, units respond maximally to dot-shaped stimuli rather than to linear stimuli as in normal cats. Pettigrew & Freeman conclude that these results "suggest that the usual high degree of specialization in cortical cells is largely derived from visual experience. Or, if the specificity is determined via innate connections, it can easily be altered to match the requirements of the early visual input". Van Sluyters & Blakemore conclude from their results that "cells in the developing visual cortex seem to have a high degree of 'adaptive' plasticity - an ability to match their properties to an unusual visual environment - that normally they would rarely be called on to employ".

One of the goals of the present study was to test the limits of early visual plasticity. The argument will be made that consideration of the anatomical organization of the visual system leads to the conclusion that the system is organized around the vertical and horizontal coordinates of visual space, and such consideration is vital for understanding how rearing cats in a visual environment consisting of vertical or horizontal lines affects development. The anatomy of the visual system will be reviewed below with the aim of illustrating how anatomical organization may determine the processing of information.

The eye can be described as a device which forms a two-dimensional spatial representation of the visual world on the surface of the retina. Analysis of the ways in which this spatial representation is modified as well as the ways in which it is preserved can perhaps provide insight into the visual process. The dynamic nature of visual processing will be ignored for the moment, i.e. the fact that the eye of the cat is constantly in motion (Pritchard & Heron, 1960; Hebbard & Marg, 1960), and that these eye movements are probably involved in the process of visual perception (Festinger, 1971). The topographic representation at several stages of the visual system will be reviewed, keeping in mind "a truism which needs repeated emphasis...that the visual system works as a whole in the mediation of visually guided behavior" (Sprague et al., 1973).

Whitteridge (1973) has stated that "the topographical representation of the retina on the visual receptive surfaces to be found in the lateral geniculate nucleus, superior colliculus and visual cortex is incomprehensible without some knowledge of the distribution of receptors and ganglion cells in the retina". In the cat, the region of maximum ganglion cell density (area centralis) occupies a roughly circular area near the center of the retina subtending a visual angle of approximately 4 degrees (Stone, 1965). Within the area centralis, the ganglion cell density is approximately 5700 per mm^2 (estimate by Sanderson, 1971 from data by Stone, 1965). The ganglion cell density decreases rapidly with increasing distance from the area centralis. The decrease in density is not symmetrical around the point of fixation, the rate being faster for temporal than nasal retina, and faster for lower compared to upper retina.

Thus, the area of the retina receiving input from the lower visual field has a higher density of ganglion cells than the area receiving input from the upper visual field. Furthermore, the area of the retina receiving input from the temporal visual field has a higher density of ganglion cells than the area receiving input from the nasal visual field. In addition to these asymmetries in ganglion cell distribution there is a relatively greater number of ganglion cells representing the horizontal meridian than any other orientation on the cat retina (Stone, 1965). Thus, if one draws isodensity lines on the surface of the retina, the area representing the highest cell density at the center of the retina is roughly circular; but with increasing eccentricity, the isodensity contours become increasingly oval shaped with elongation along the horizontal meridian.

Information leaves the retina via the optic nerve which "is composed chiefly and perhaps exclusively of the axons of retinal ganglion cells" (Meikle & Sprague, 1964). Figure 1 roughly summarizes the retinotopic organization of major visual structures in the cat.

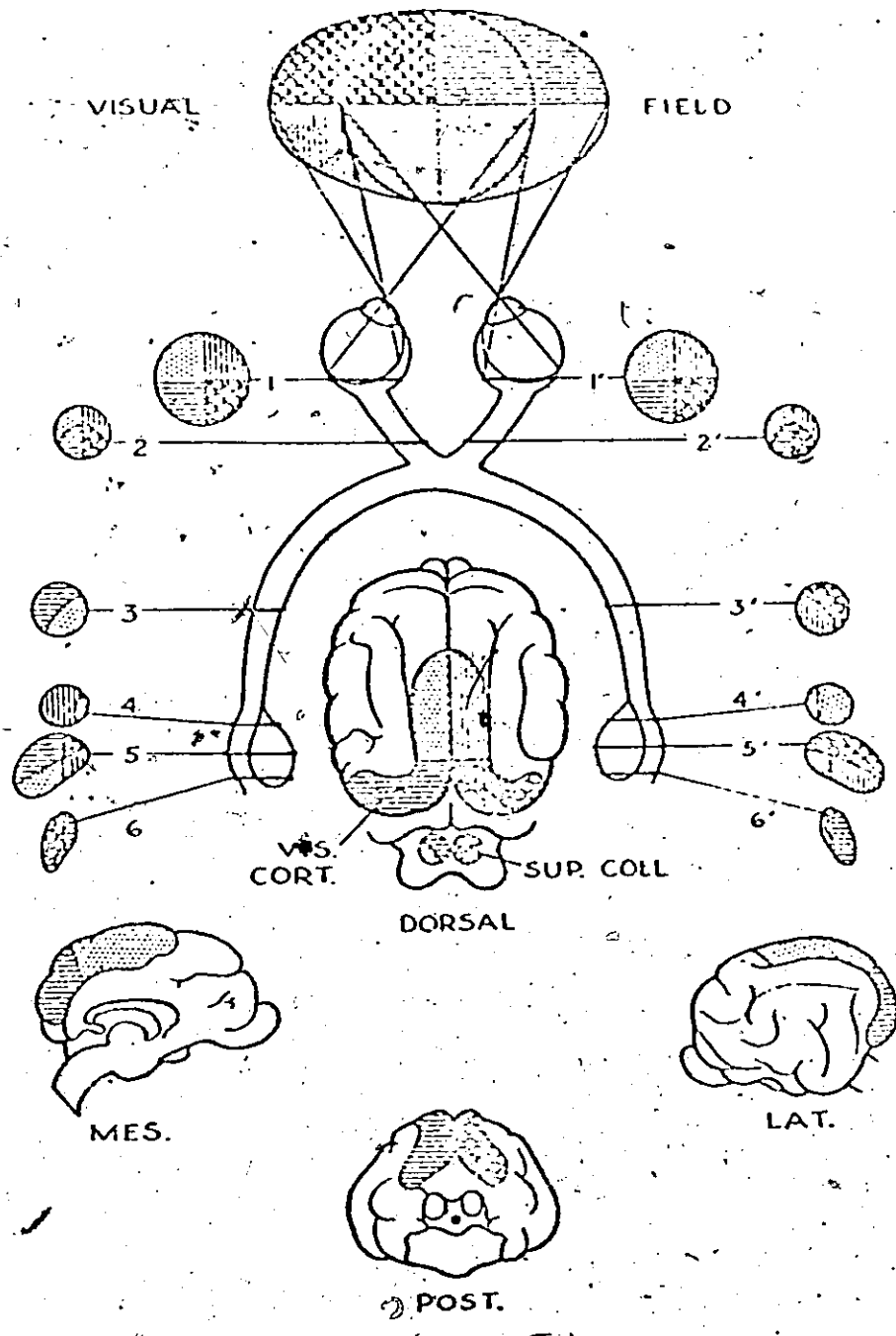
Fibres from the retina terminate in at least five areas in the cat (Sprague, et al., 1973). These are: 1) dorsal lateral geniculate nucleus of the thalamus (LGNd), 2) ventral lateral geniculate nucleus (LGNv), 3) nucleus of the optic tract and pretectal nuclei, 4) superior colliculus (SC), and 5) accessory optic nuclei. Only the major connection to LGNd will be considered here.

It has been estimated that approximately 80% of optic tract fibers terminate in the dorsal lateral geniculate nucleus (von Monakow, 1905 cited in Meikle & Sprague, 1964). In the cat, the LGNd is a clearly

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Figure 1. Retinotopical organization of the visual system of the cat

(chiefly from Apter, 1945; Hoessly, 1947, Overbosch, 1927, Talbot and Marshall, 1941). It should be pointed out that the data on the optic nerve, optic tract, and lateral geniculate nucleus are derived from anatomical studies, and those on the striate cortex and the superior colliculus are derived chiefly from electrophysiological work. The representation of all 4 retinal quadrants in each lateral geniculate nucleus is explained by the fact that Overbosch divided the retina by means of lines drawn through the optic disc rather than through the area centralis. Had he used the area centralis, presumably each lateral geniculate nucleus would receive fibers from only 2 retinal quadrants, as is shown in this figure for the optic tract and the striate cortex. Transverse sections: (1,1') retina; (2,2') optic nerve; (3,3') optic tract; (4,4') rostral part of lateral geniculate nucleus; (5,5') medial part of lateral geniculate nucleus; (6,6') caudal part of lateral geniculate nucleus. Lat.: lateral view of left cerebral hemisphere. Mes.: mesial view of left cerebral hemisphere. Post.: posterior view of cat's brain with midbrain transected below the inferior colliculi. Sup. Coll.: Dorsal view of superior colliculi. Vis. Cort.: Visual cortex indicated on dorsal view of cerebral hemispheres. (From Meikle, and Sprague, 1964)



laminated cell sheet consisting of three main layers: A, A₁, and B (Szentagothai, 1973). Input to the layers of the LGNd is segregated with respect to eye of origin. The discussion here will be, mainly concerned with the connections to layers A and A₁. There is anatomical and physiological evidence (reviewed by Freund, 1973) that layer B or its subdivisions is organized somewhat differently than the other two geniculate layers.

In addition to segregating with respect to eye of origin, optic tract fibers are also distributed retinotopically. Bishop, Kozak, Levick and Vakkur (1962) were the first to demonstrate, with electrophysiological techniques, the nature of the point-to-point projection of the retina on the surface of the LGNd in the cat. These authors found that the nasal retina of the contralateral eye is mapped on the surface of layer A of the LGNd in such a way that the central area of vision is effectively magnified in terms of area on the LGNd per degree of visual angle. They also found that the lower field is represented by an area about twice that devoted to the upper field. Bishop, et al suggested that the differential representation of the visual field in the LGNd is related to ganglion cell density differences in the retina. A similar conclusion is reached by Sanderson (1971) on the basis of his correlations of known ganglion cell densities (Stone, 1965) and LGNd magnification factors. Sanderson also points out that whereas cell density varies spatially across the retina, the distribution of cells within geniculate lamina, as well as the optic tract terminal distribution, is fairly uniform. Thus, it seems likely that the effective magnification of the visual field which occurs at the LGNd is the result of the uniform distribution of retinal

afferents. In other words, the differential distribution of retinal ganglion cells can be said to constitute a potential magnification of the visual field which becomes manifest when the fibers are distributed in the target structure.

The mapping performed by Bishop et al revealed not only that there is a functional projection of the retinal surface in the LGNd, but also that the projection is highly organized within the nucleus. The retinal projection to the LGNd is arranged in such a way that the vertical and horizontal coordinates of the visual field are preserved as planes within the nucleus. Figure 2 shows this organization. All points on a line running from anterior to posterior within the nucleus receive input from points in the visual field which are equidistant from the vertical meridian. Though the particular mapping obtained by Bishop et al is to some extent an artifact of the coordinate system used to map the retina (Bishop, Kozak, & Vakkur, 1962), the fact that vertical and horizontal coordinates of the visual field are revealed as orthogonal planes in the geniculate suggests the possibility that there are underlying fiber tracts which retain this information.

Following the complex transforms of information which take place as a result of the distribution of fibers of retinal origin within the LGNd and other subcortical visual nuclei, cells of these nuclei send fibers of their own to the cortex. Within the cortex, further retinotopic subdivision of input occurs and fibers are sent back to the subcortical nuclei of origin as well as to other cortical and subcortical locations.

The visual cortex of the cat has been divided into six main laminae (for details of lamination and sublamination see Szentagothai

1973). In addition, the primary visual cortex has been subdivided into three areas on the basis of morphological criteria: 17, 18, and 19 (Otsuka & Hassler, 1962: cited in Garey & Powell, 1967). Whitteridge (1973) points out that "in the cat area 17 is twice the sum of areas 18 and 19 but in man areas 18 and 19 are three times the size of 17". In the cat, a fourth cortical area receiving visual projections occurs in the lateral suprasylvian gyrus. The four visual cortical areas are roughly side by side on the posterior surface of the cortex of the cat, area 17 is on the midline and areas 18, 19 and the suprasylvian gyrus are increasingly lateral.

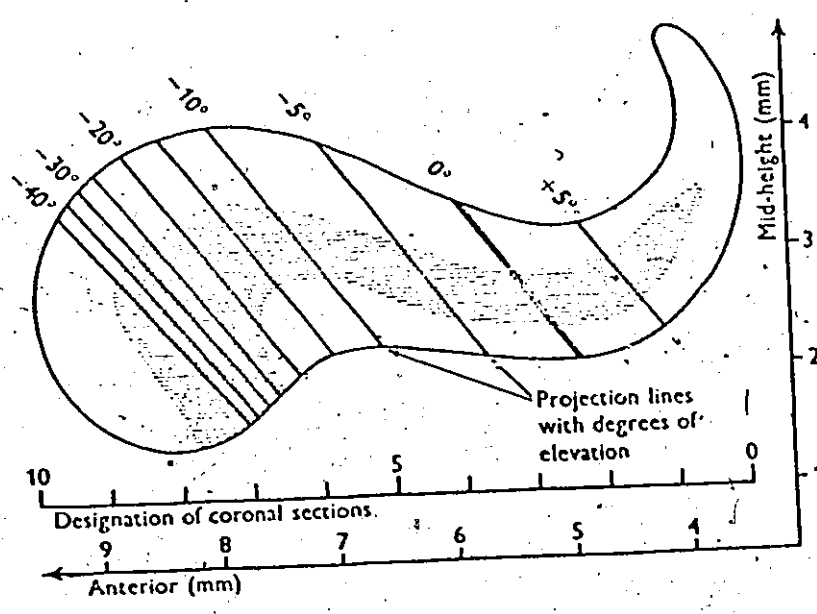
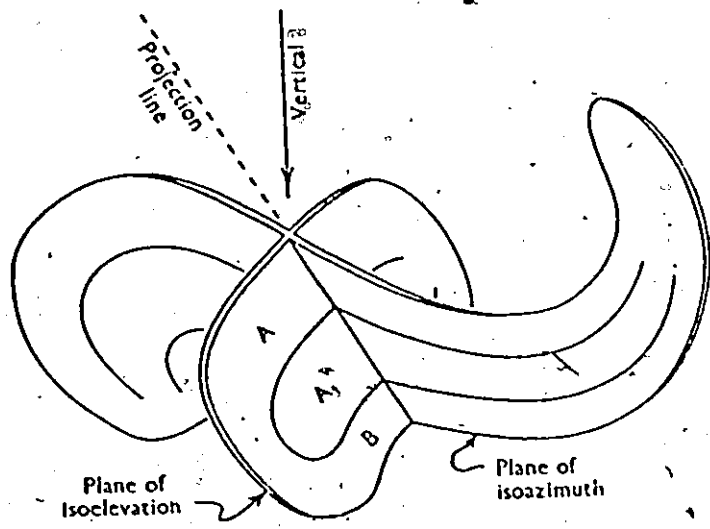
It has been shown that projections to cortical visual areas are topographically arranged with the result that there are at least four maps of the contralateral visual field on the surface of the cortex (reviewed by Whitteridge, 1973). Garey & Powell (1967) explored the nature of cortical projections by tracing patterns of degeneration following specific cortical lesions. These authors determined that areas 17 and 18 receive projections from the main laminae of the LGNd. Area 19 receives projections from the medial intralaminar nucleus, a nucleus which is part of the lateral geniculate complex and which receives a separate retinotopic projection. The suprasylvian gyrus seems to receive collaterals from afferents to the other cortical areas. It is generally held that the retinotopic map on area 18 is a mirror image of the map on area 17 which is situated just medial to it (see review by Whitteridge, 1973). Garey & Powell showed that the projection from the LGNd to area 17 is inverted with respect to the position of the vertical meridian. While the vertical meridian is represented on the medial aspect of the LGNd,

the vertical meridian forms the lateral boundary of area 17. The projection to area 18 from the large cells of the LGNd retains the spatial arrangement of the geniculate. Thus, the vertical meridian forms the medial boundary of area 18. The result of this arrangement is that the vertical meridian is represented twice at the interface of area 17 and 18. Points either more medial or more lateral to this interface represent points in the visual field of increasing eccentricity. It is suggested here that this mirror image effect results from the differential projection of fibers representing the vertical and horizontal planes in the visual field.

The projections to areas 17 and 18 preserve the magnification of the central part of the visual field noted in the LGNd. Garey & Powell (1967) found that the antero-posterior plane of the LGNd is also preserved in its projection to the cortex. Thus the anterior portion of the LGNd projects to the anterior poles of areas 17 and 18, while the posterior portion of the LGNd projects to the caudal poles of areas 17 and 18. It should be recalled (Figure 2) that planes in the LGNd running from medial to lateral, represent points in the visual field which are equidistant from the horizontal meridian. The lower part of the visual field is represented in the anterior portion of the nucleus while the upper field is represented posteriorly. The result of the geniculo-cortical projection is that horizontal planes in the visual field are represented in the same way in areas 17 and 18. The lower part of the visual field is represented in anterior portions of these areas, while the upper part of the field is represented posteriorly on the cortex. The inversion of the projections to 17 and 18 occurs around the vertical meridian, leaving the horizontal meridian

Figure 2. Semi-schematic drawings of the projection of the visual field on the parasagittal plane of the LGNd of the cat. Upper: semi-schematic perspective drawing showing planes of isoazimuth and isoelevation in the left LGNd intersecting along a projection line. The planes are viewed from a point posterior, lateral and slightly above the nucleus. A, A₁ and B, principal cellular laminae in the LGNd. Lower: semi-schematic parasagittal section through the centre of the LGNd showing location of some selected projection lines. Outer scales indicate the anterior and superior H-C co-ordinates. Inner scale defines planes through the LGNd for the purposes of visual field mapping. (From Bishop, Kozak, Levick, and Vakkur, 1962)

All points on a plane of isoelevation are equidistant from the horizontal meridian through the center of the area centralis, while all points on a plane of isoazimuth are equidistant from the vertical meridian through the center of the area centralis.



relatively intact.

Some aspects of the anatomy of visual connections from retina to cortex have been reviewed. This review has revealed the visual system as a highly organized structure. The connections from the receptor surface retain their spatial positions at each level in the system. An intriguing aspect of these connections is that horizontal and vertical components of the field representation appear to be organized differently. The initial segregation of horizontal and vertical components which occurs in the LGNd is reflected in the cortex by differential projection of these components which modifies one but leaves the other intact. Further evidence for the separability of horizontal and vertical components of the visual projection comes from a situation where the mechanism of visual development malfunctions resulting in an abnormal visual anatomy.

In the siamese cat, an abnormality occurs in the projection from the retina to LGNd (Guillery & Kaas, 1971). The siamese abnormality occurs in the fibers from the ipsilateral temporal retina which normally innervate layer A1 of the LGNd. A portion of these fibers representing a region of retina within 20° of the vertical meridian crosses at the optic chiasm and innervates the contralateral rather than the ipsilateral LGNd. It appears that although the fibers are misrouted, they innervate the contralateral LGNd in the same way that they would have innervated the ipsilateral LGNd. Thus, these fibers segregate from those fibers which arise from the nasal retina. The nasal retinal fibers decussate normally at the

optic chiasm to achieve a normal innervation pattern. The aberrant fibers arrive in contralateral layer A1 and distribute themselves in this layer in approximately the same medio-lateral and antero-posterior position that they would have occupied in the normal ipsilateral A1. The result of this distribution of fibers is that in the siamese cat the aberrant connections to lamina A1 in the LGNd are at the normal antero-posterior plane but are at an abnormal medio-lateral plane of the nucleus. In addition, layer A1 which normally contains a representation of the contralateral visual field, contains a representation of portions of the ipsilateral visual field in siamese cats. If single units are recorded from the LGNd in siamese cats the receptive fields of cells in abnormal lamina A1 are at the same horizontal position in the visual field as the fields of cells recorded at a corresponding point of lamina A (Guillery & Kaas, 1971; Hubel & Wiesel, 1971). The fields recorded from lamina A are however on the contralateral side of the vertical meridian, whereas the fields recorded from lamina A1 are approximately an equal distance on the ipsilateral side of the vertical meridian.

Thus, the siamese abnormality selectively affects the location of the retinal projection with respect to the vertical meridian and does not at all influence the projection with respect to the horizontal meridian. The fact that the siamese anomaly differentially affects the vertical and horizontal coordinates of the visual field representation in the LGNd suggests that these coordinates are important in the initial structuring of retinotopic projections to the geniculate.

Data from another species also suggests that the horizontal and vertical coordinates of visual space can be specified separately in a visual system.

Jacobson, (Reviewed in Edds, Barkley & Fambrough, 1972) studied the development of the visual system in the clawed frog Xenopus Laevis. By electrophysiologically mapping the projections from the retina to the tectum, he has discovered that if the eye primordium is inverted in an early-tailbud stage embryo and the animal allowed to develop, the retinotectal projections are similar to those seen in a normal animal. That is, rotation has occurred before connections have been specified and new connections have distributed themselves according to the new eye position. On the other hand if the eye is inverted in the late tailbud stage, the retinotectal projections of the adult animal are completely inverted, presumably because the eye inversion has occurred after the specification of connections. A surprising result is that in some cases where the eye is inverted in an intermediate tailbud stage, the retino-tectal connections of the adult are found to be normal along the vertical axis of the retina but inverted along the horizontal axis. An interpretation of this result is that retino-tectal connections in Xenopus develop first along the horizontal axis and then along the vertical axis.

One can only speculate as to the mechanism or function of separate axis specification in visual systems. Presumably this phenomenon reflects differential growth rates along the antero-posterior and medio-lateral planes of the organism. Perhaps the separate specification of visual axes simplifies the process of preserving complex spatial arrangements in the visual system. The horizontal axis may first be specified as a kind of warp on a neural loom through which is woven the complexity of visual integration. Visual input might stabilize this pattern which is loosely specified at birth.

Regardless of the mechanism or function of the separate specification of orthogonal visual axes it can be concluded that such a pattern of development can occur, and that the result of this pattern of development would be a visual system essentially organized around the vertical and horizontal coordinates of visual space. The utility of such an arrangement is unclear. However, it may be that the early segregation of horizontal and vertical visual axes is important for the oculomotor control system. There is much clinical evidence that horizontal and vertical eye movements are separately controlled in the human (Duke-Elder, 1962). In addition it has recently been suggested on the basis of single unit recording in alert monkeys that visual information goes through a horizontal-vertical coordinate system before reaching the extra-ocular muscles (Westheimer & Blair, 1972). Finally, Goodwin and Fender (1973) have concluded on the basis of observations of eye tracking tasks in humans that "the oculomotor system can be described as having independent vertical and horizontal channels with relatively small mutual cross-talk".

Evidence has been presented in support of the idea that as a result of the specific, highly organized pattern of nerve connections in the visual system, the representations of the vertical and horizontal coordinates of visual space are separately specified and organized. In the present study we sought to determine whether there are constraints on the early plasticity of the visual system which are consistent with this idea. Specifically, we wondered whether early visual experience limited to vertical or horizontal lines affects the visual system in a way which is different from early experience limited to oblique lines.

In order to investigate the general role of input in modifying

visual function, we measured apparent output parameters of visual function as well as input parameters.

In addition to a possible role in the process of information extraction (Festinger, 1971; Noton and Stark, 1971), the oculomotor system can be said to serve at least three broad functions in the visual process. One involves the maintenance of physical alignment between the receptor surfaces of the two retinas which is necessary for binocular vision. A second is to move the receptor surfaces in ways which allow new information to be brought onto the specialized central portion of the retina, or keep information from moving stimuli on this central portion. Third, eye movements serve to provide change in the stimulus array which is necessary to prevent the array from fading (Pritchard, Heron, & Hebb, 1960).

Most of what is known about the effects of early visual input on oculomotor function concerns the eye alignment system. Before considering this evidence it might be useful to consider the nature of binocular integration.

In normal binocular vision a single stimulus object forms two images; one on each retina. The information contained in the separate neural representations on each retina must somehow be integrated to form the neural basis of a single binocular percept. Part of the process of normal binocular integration must involve the physical alignment of the visual axes so that images of a stimulus object fall on corresponding points of the two retinas.

Sherman (1972) provides the only available information about the normal development of the alignment function in cats. He found that at

the time of eye opening cats have a large divergent strabismus, which remains until the fourth postnatal week, when occasional periods of eye alignment begin to occur. These periods increase in frequency until by about the seventh week fluctuations in eye alignment cease, and normal, stable, interocular alignment is achieved.

Sherman found that the development of normal interocular alignment occurred even in animals that had bilateral visual cortex lesions before the time of normal eye opening. The work of Hubel & Wiesel (1965) suggests that the presence of binocularly active single units in the visual cortex is not a necessary correlate of alignment. These authors raised two kittens with alternate day monocular occlusion from the time of normal eye opening to an age of ten weeks. Thus, although these animals received input to both eyes during development, they never received binocular input. Just as in animals with artificial squint, who are deprived of simultaneous aligned binocular input by cutting the medial rectus eye muscle, there was an absence of binocularly active single units in the visual cortex of these animals. However, Hubel and Wiesel report that there was no apparent strabismus. Thus, the presence of simultaneously corresponding input to the two retinas does not seem to be necessary for the development of eye alignment, though such input is necessary for the development of binocular cortical units.

Several procedures have been found to result in abnormal interocular alignment. Sherman (1972) found that animals prevented from seeing during the first six months of life by either monocular or binocular lid suture develop squint, divergent in binocularly sutured animals, but either divergent or convergent in monocularly sutured cats.

Squint also develops in the presence of certain types of binocular input. It has been found that kittens raised under strobe-light illumination usually develop ocular deviations (Karel Gijbers, unpublished observation). In addition, cats raised by Hirsch and Spinelli (1970, 1971) viewing stimulus patterns mounted in goggles (vertical lines in one eye and horizontal lines in the other) developed squint. The divergent squint of this latter group of animals was found to be lessened after long periods in a normal environment (Spinelli, et al., 1972). Finally, it has been implied by Van Sluyters and Blakemore (1973a) that animals raised with visual exposure limited to binocular viewing of parallel horizontal or vertical lines (Blakemore and Cooper, 1970, 1971) develop abnormal interocular alignment.

It is of interest that squint produced in normal animals by abnormal visual input has been found (Sherman, 1972; Spinelli et al., 1972; Van Sluyters and Blakemore, 1973) to be maintained when the extraocular muscles are paralyzed, suggesting that the effect of early input is to change the resting lengths of the muscles so that the system achieves a new steady state.

Support for the role of early input in determining relative eye position comes from an observation by Hubel and Wiesel (1971). These authors raised a siamese kitten in the dark. Though all the litter mates and both parents of this animal had marked squint, it did not develop squint. This suggests that the squint of some siamese cats is secondary to their aberrant visual connections; those connections in interaction with a normal visual environment produce eye deviation. A further aim of the present study was to investigate how abnormal visual

input produces squint in a normal animal. By looking at the differential effects of different types of early visual input on eye alignment we hoped to gain insight into the process by which the eyes become aligned.

Little is known about development of the eye movement systems in cats. Riesen (1961) reports that monkeys raised in the dark develop a jerk-type nystagmus, but nothing is known about the effects of specific input on the eye movements of adult animals. A final aim of the present study was to investigate this relation in cats.

Thus, the aim of the present series of experiments was to answer two broad questions. These are: 1) Does early visual input modify motor functions of the visual system? and 2) Does input restricted to either the vertical or horizontal coordinates of visual space modify the system differently from input restricted to some other visual orientation?

Oculomotor Function

Methods

Eighteen kittens from six litters were reared under conditions of restricted visual input. The distribution of animals from different litters into different experimental conditions is shown in table 1.

The apparatus used was similar to that described by Blakemore and Cooper (1970). The kittens were placed in a vertical cylinder (1.8 m. tall and 45 cm. in diameter) and were supported by a glass plate .9 m. from the floor which was illuminated from above by two 60 watt incandescent bulbs, diffused by a translucent white screen placed over the top of the tube. The luminance of the stimulus patterns which were mounted on the inside of the cylinder was approximately 10 millilamberts for white parts of the pattern and 0.1 millilamberts for black parts, at the level of the kitten. The patterns consisted of alternating black and white stripes whose widths ranged from 1 cm. to 5 cm. arranged in a semi-random order.

Two kittens (H-1 and H-2) had the stripes oriented horizontally, four (V-1, V-2, V-1B, and V-2B) had the stripes arranged vertically, and four (O-1, O-2, O-1B, and O-2B) had the stripes oriented at 45° from the horizontal. Several control conditions were used: for two animals (Di-1 and Di-2) the inside wall of the cylinder was covered with plain white paper, one kitten (MO-1) was exposed to a random array of lines of different widths and orientations on the inside wall of the cylinder, and three animals (RC-1, RC-2, and RC-3) were kept in the dark as were the other animals but were put in restriction tubes which had walls made out of clear plastic film allowing the animals to see the room. A dark reared animal (Da-1) was kept in the dark during the entire rearing

• Table 1. Rearing conditions of kittens. Oculomotor function of litters
1 and 2 was tested after 2 months post-restriction dark experience plus
18 months in a normal laboratory environment. Oculomotor function of
litters 3-6 was tested immediately after restriction. Unit recordings
were made after 2 years in a normal laboratory environment for litters
1 and 2, and after 4 months for litters 3-6.

Table 1

Litter Number	1	2	3	4	5	6
Horizontal	H-1	H-2	V-1B V-2B			
Vertical	V-1	V-2		O-1B* O-2B		
Oblique	O-1	O-2				
Diffuse control	DI-1	DI-2				
Dark control	Da-1					
Unrestricted control			UNRC-1			
Restricted control						RC-1 RC-2 RC-3
Multi-orientation control					MO-1	

* At end of restriction this animal was found to have the blue iris and red retina characteristic of albino animals. O-2B had no overt signs of albinism.

period, while an unrestricted control animal (UNRC-1) was allowed to freely explore the laboratory while its littermates received restricted visual input.

All kittens were housed in a cage with their mothers in a completely dark room before their eyes opened. Beginning at four weeks of age each kitten, except animal Da-1, received approximately 3 hours per day of visual experience, six days a week. While in the restriction tubes each kitten wore a white paper neck ruff (Hein and Held, 1967) to prevent it from seeing itself. Animals were transported from the dark room to the rearing apparatus with an opaque hood over their heads and precautions were taken to avoid any visual input other than that received from the stimulus patterns in the apparatus.

All animals received restricted visual experience from 28 days to 90 days of age. Kittens from litters 1 and 2 spent the next two months in the dark room and the following 18 months, uncaged, in a room in the laboratory after which their eye movements were measured. The eye movements of kittens in litters 3, 4, 5, and 6 were measured 24 hours after the last period of restricted visual experience at the end of the third month.

The most sensitive technique used to record eye movements was a modification of the light lever procedure used previously (Pritchard and Heron, 1960; Hebbard, and Marg, 1960) to record small eye movements in cats.

The animal was held in a restraining box having a movable side wall which could be adjusted so that each animal fitted snugly in the narrow box. The animal's head was held in a stock which restricted movement at

the neck but allowed the head to turn freely, and a foam pad between the back of the animal and the sliding roof of the box controlled back movements. Held in this way, firmly yet with no painful pressure, all animals adapted to restraint within 15 minutes. Many animals, especially after having been in the restraining apparatus a number of times, purred while measurements were being made.

After the cat was restrained, the lids of both eyes were gently retracted and phenylephrine (Neosynephrine) was placed on the right eye to relax the nictitating membrane. A local anaesthetic (Pontocaine) was also placed on the eye followed by methyl cellulose (Isopto tears) which had been allowed to become tacky, and then a small square of tissue (about 2 x 2 mm.) was placed just lateral to the limbus. A mirror chip (about 1 x 1 x .1 mm.) which had previously been coated on the underside with paraffin wax to blunt sharp edges was then placed on the center of the tissue. The cat was then manoeuvred so that the mirror on the eye was at a focal point of an optical system consisting of a collimated light source, target pattern of vertical lines, and a lens which brought the image of the target into focus, after being reflected from the eye mirror, on a tangent screen placed approximately 1 meter from the cats eye. Auxilliary mirrors in the light path allowed for final modification of the position of the projected image, and a series of parallel horizontal cylindrical lenses placed in front of the tangent screen produced final intensification of the image pattern. A Grass C-4 camera on the far side of the tangent screen was used to record the rear projected pattern of image movements on a continuously moving strip of film. The smallest movement which could be recorded with this system was approximately 30 minutes of arc.

Two animals were prepared for chronic eye movement recording at the end of single unit experiments. The animals were re-anaesthetized with Halothane anaesthesia and holes were drilled above the left and the right frontal sinuses. Two small jewellers screws were inserted in the bone of the orbit along the medio-lateral plane of each eye, and screws above the frontal sinuses served as indifferent electrodes. Leads which had previously been soldered to the screw electrodes were fixed to an Ampex connector and the entire assembly was fixed rigidly to the skull with dental acrylic.

A standard recording situation was used to record eye movements from the implanted bone screws. Electrical activity was either recorded on an AC-coupled polygraph (Beckman) for visual analysis, or on an FM tape recorder (Ampex SP-300) for computer analysis.

Results

I. Observations on normal development

Before turning to the effects of restricted visual input on oculomotor function some aspects of the normal pattern of visual development in the cat will be described. These observations were made because little is known about normal visual development and it was felt that such information would be useful in studying the effects of early restriction.

In addition to general observations, the development of two forms of visually guided behavior were tested in 3 kittens at two day intervals from day 28 to day 60. Visual placing was tested by holding the animal in such a way that the hind legs were firmly yet gently restrained and the forelegs were free to move. The animal was moved slowly toward the edge of a table, and a positive response was recorded if the animal extended its forelegs before touching the table edge. Ten consecutive trials were run on each testing day, with an inter-trial interval of approximately 30 seconds.

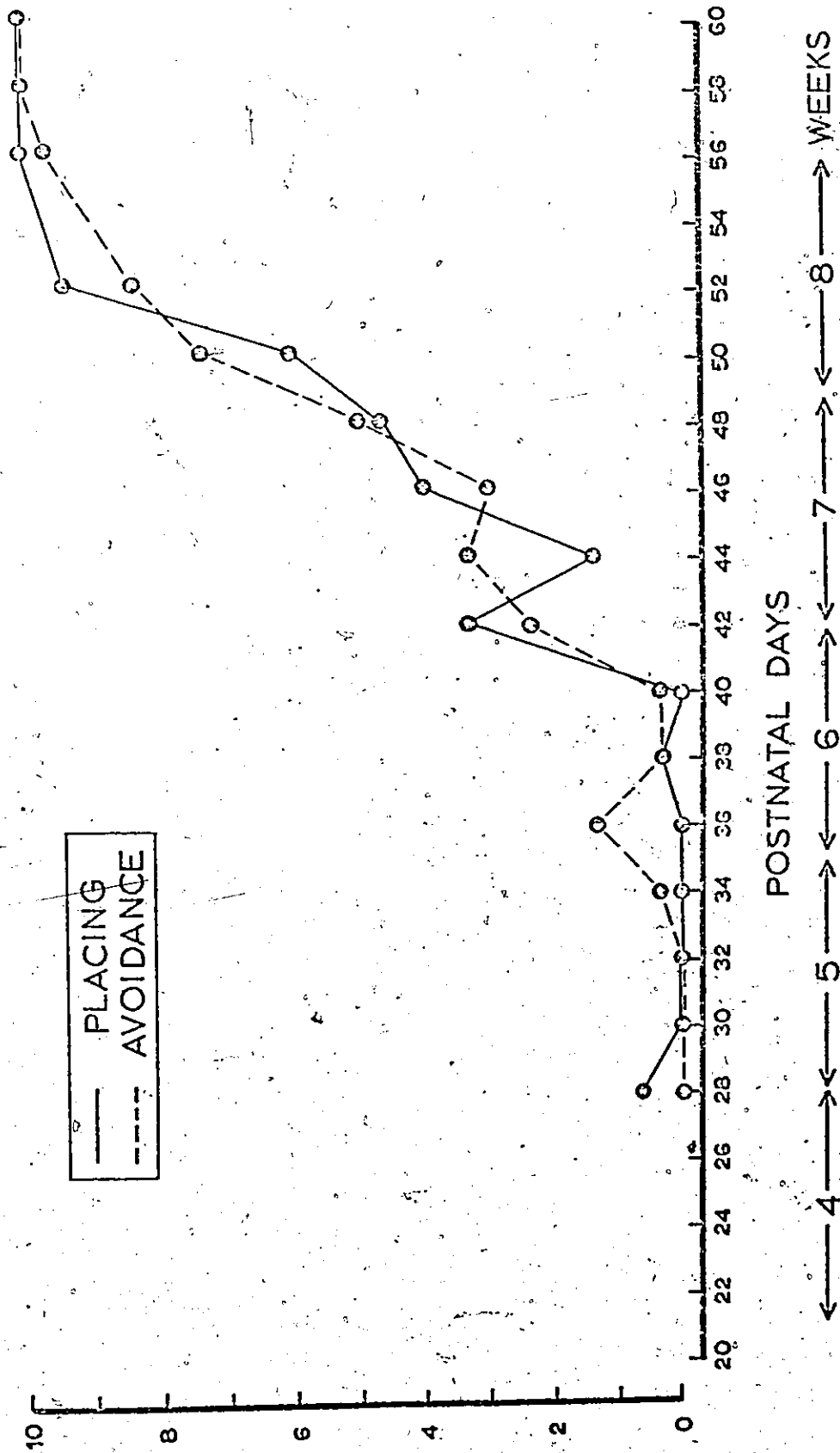
In the visual avoidance test a single trial consisted of holding the animal gently in one hand and slowly moving the other hand toward the animals eyes. A positive response was any movement related to the approaching stimulus, such as an eye blink, head movement, or face twitch. Ten trials per testing day were also run with this test, and the inter-trial interval was again about 30 seconds.

Figure 3 shows that both visual placing and visual avoidance develop at approximately the same rate. A striking aspect of this developmental picture is that though the kittens eyes were open by, approximately the twelfth postnatal day, the animals were unresponsive

Figure 3. Mean scores on two tests of visually guided behavior (N=3).

Positive response criteria for each test described in text.

AVERAGE NUMBER OF POSITIVE RESPONSES



in the test situations until the end of the fourth postnatal week and not until the ninth postnatal week was normal responsiveness attained.

It is probably relevant that the ability to stand was not reliably present until the fifth postnatal week.

The basic results described above are in agreement with observations by the author on at least 25 developing kittens born in the laboratory and at home. In addition, other workers have less systematically described much the same sequence of events (Windle, 1930; Norton, 1972; Sherman, 1972).

The development of eye movements was observed in a total of eight kittens from three litters. Following eye opening, which occurred between day eight and day twelve, the eyes of all kittens were found to be diverged slightly. In general, no gross eye movements were observed at this stage except for occasional upward slow drifts which occurred at approximately the same time in both eyes. To quantify these observations filmed records were obtained with the optical lever technique. These showed that the drift rate was about one degree per second. The drifts always moved upward, never left to right, and the slow phase of these movements was always up, followed by a rapid return. No fixation or following movements could be elicited at this stage.

Initially, we planned to measure eye movements repeatedly during development using the optical lever technique. It soon became clear however, that while the measurements seemed valid for the early observations, the measuring technique was distorting eye movement patterns in later stages of development. It was found that removing the kitten from the company of its mother and restraining it so as to obtain extremely precise eye

movement measures resulted in two general types of response. The animal either struggled violently and meowed continually or else assumed an apparently non-reactive state during which the eyes would diverge if they had been aligned and the kitten would become unresponsive to stimuli though a sluggish pupillary response would be present.

As a result, eye movement patterns were subsequently observed in kittens which were either gently held in a normally lighted room or placed in a standard viewing situation consisting of a wooden enclosure (80 x 45 x 50 cm.) placed on a firm table top, open in front and illuminated by a 60 watt incandescent bulb. Eye alignment was assessed by a light reflex technique (Sherman, 1972) in which the animal was held at arms length while the experimenter moved a small bright source of light to induce fixation. The reflection of the light source with reference to the vertical slit of the cats pupil was used as an indication of the relative alignment of the optic axes. In kittens older than about 20 days eye deviations as small as 7° can be discriminated with this technique (Sherman, 1972) and registered on film (figure 4). In kittens younger than 20 days accuracy is reduced because pupillary constriction is incomplete.

The general pattern of eye alignment and eye movement observed at the time of eye opening remained apparently unchanged until the fourth postnatal week. At this time occasional periods of eye alignment were observed and conjugate saccadic eye movements were noted appearing in all animals, though they would often not fixate or follow a moving target with their eyes, even if it were a novel one. During weeks 4-8 conjugate fixation eye movements could be elicited only during periods

Figure 4. Interocular alignment of normal adult cat. The animal is facing a light source directly behind the camera and the degree of alignment can be assessed by the relation between the light source reflections in the cat's eyes and the centers of the pupils.



INTEROCULAR ALIGNMENT OF NORMAL
ADULT CAT

when eye alignment was observed. These periods became more frequent as the animal got older, but it was often observed that animals which displayed consistent eye alignment and fixation movements on one day might on the next show neither. Why this was so is not readily apparent though as noted above, attempts to restrain the animal often caused the eyes to diverge. By the eighth postnatal week the eyes of all animals were found to be consistently aligned and they would fixate and follow a target with their eyes. Eye movements recorded at this stage were at least grossly similar to the eye movements of adult animals.

II. Effects of specific early input on oculomotor function

A sample of oculomotor activity recorded by the optical lever technique from a normally reared adult cat is presented in Figure 5 to provide a comparison with the abnormal activity to be described below. This sample shows a saccadic movement followed by a single long fixation which is terminated by another saccadic movement. Although the fixation in this sample is greater than fifteen seconds long, this is not abnormal for a cat (Pritchard & Heron, 1960; Hebbard & Marg, 1960). Of special relevance here is the stability of eye fixation. Though there are slight drifts from the beginning to the end of fixation, the eye remains remarkably stationary throughout the period between saccades.

A. Pendular nystagmus

In contrast to the stability of eye position in a normal cat, Figure 6 shows two samples of eye movement recorded from cat H-2 eighteen months after restriction. This animal has developed a pendular nystagmus which has variable amplitude and frequency. The eye movements in this animal and similar animals appeared to be largely torsional, however the

Figure 5. Eye movements of a normal adult cat during visual fixation.

In this figure, and in figures 6, 7, and 8, filmed records are shown of the horizontal component of right eye movements measured by the optic lever technique described in the text.

FIXATION EYE MOVEMENTS OF A NORMAL CAT - CONTINUOUS RECORD

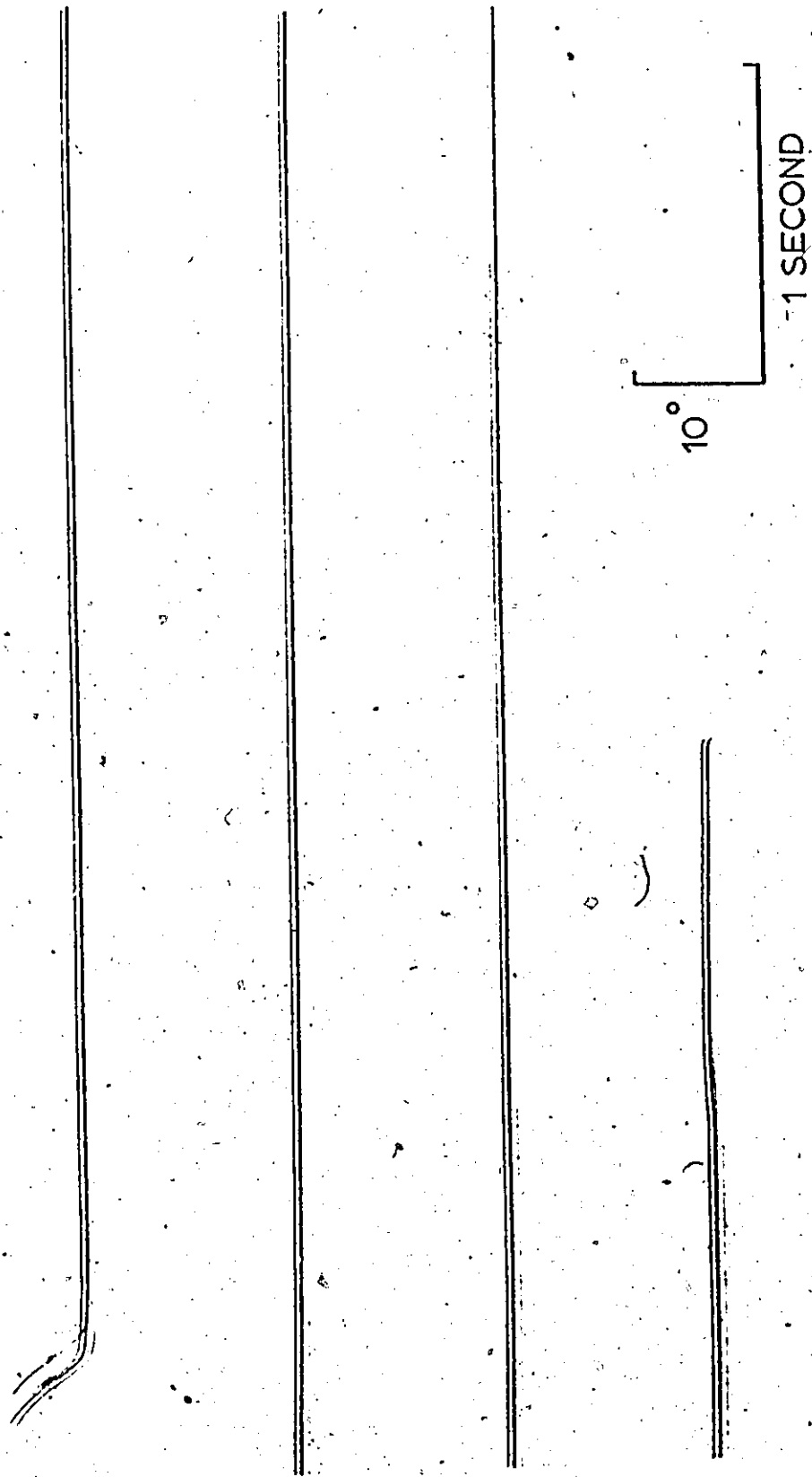
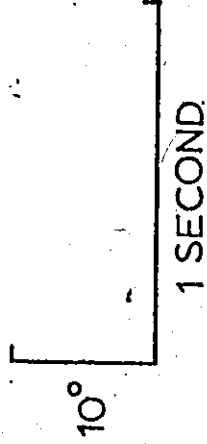
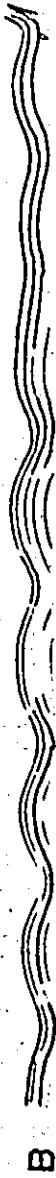


Figure 6. Typical sample eye movements of a restricted animal during visual fixation.



FIXATION EYE MOVEMENTS OF A RESTRICTED ANIMAL



ANIMAL H-2

measurements reported here are concerned mainly with the horizontal component of these movements.

Though the nystagmus observed in Figure 6 is an extreme example in terms of amplitude, similar patterns of eye movement were seen in all restricted animals, and further examples are shown in figure 7. In general, it seemed that nystagmus was more marked in cats which had been put in the dark for two months after restriction and then lived in the laboratory for 18 months, than in cats which had just come out of restriction. Further, it appeared that the tremor in the latter group increased during the four month period after restriction.

These abnormal eye movements occurred in bursts lasting 4-10 cycles (see figures 6 and 7A) with a frequency varying from 3-5 Hz. The bursts generally began with high frequency, high amplitude movements, and both amplitude and frequency gradually decreased. A summary of the eye movement parameters measured by the optic lever technique along with a comparison of normal human and normal cat eye movement parameters is shown in table 2. Pendular nystagmus was least severe in the animals reared with oblique visual input.

It should be noted that nystagmus appeared to be influenced by the measuring process. That is, while the experimenter could see it occurring when the cat was unrestrained, it frequently disappeared when the cat was in the apparatus for measuring eye movement using the optical lever technique. An example of this is shown in eye movement records obtained by the optic lever technique in animal H-1 (figure 8). Electro-oculographic (EOG) recordings from this animal are shown in figure 9 which illustrates that large amplitude nystagmus was present in H-1 when it was unrestrained.

Table 2. Summary and comparison of eye movements parameters. Data for restricted animals obtained from filmed records of the horizontal component of eye movements measured by the optic lever technique. Drift velocity was determined from estimates of the mean eye position.

Table 2

Summary and comparison of eye movement parameters.

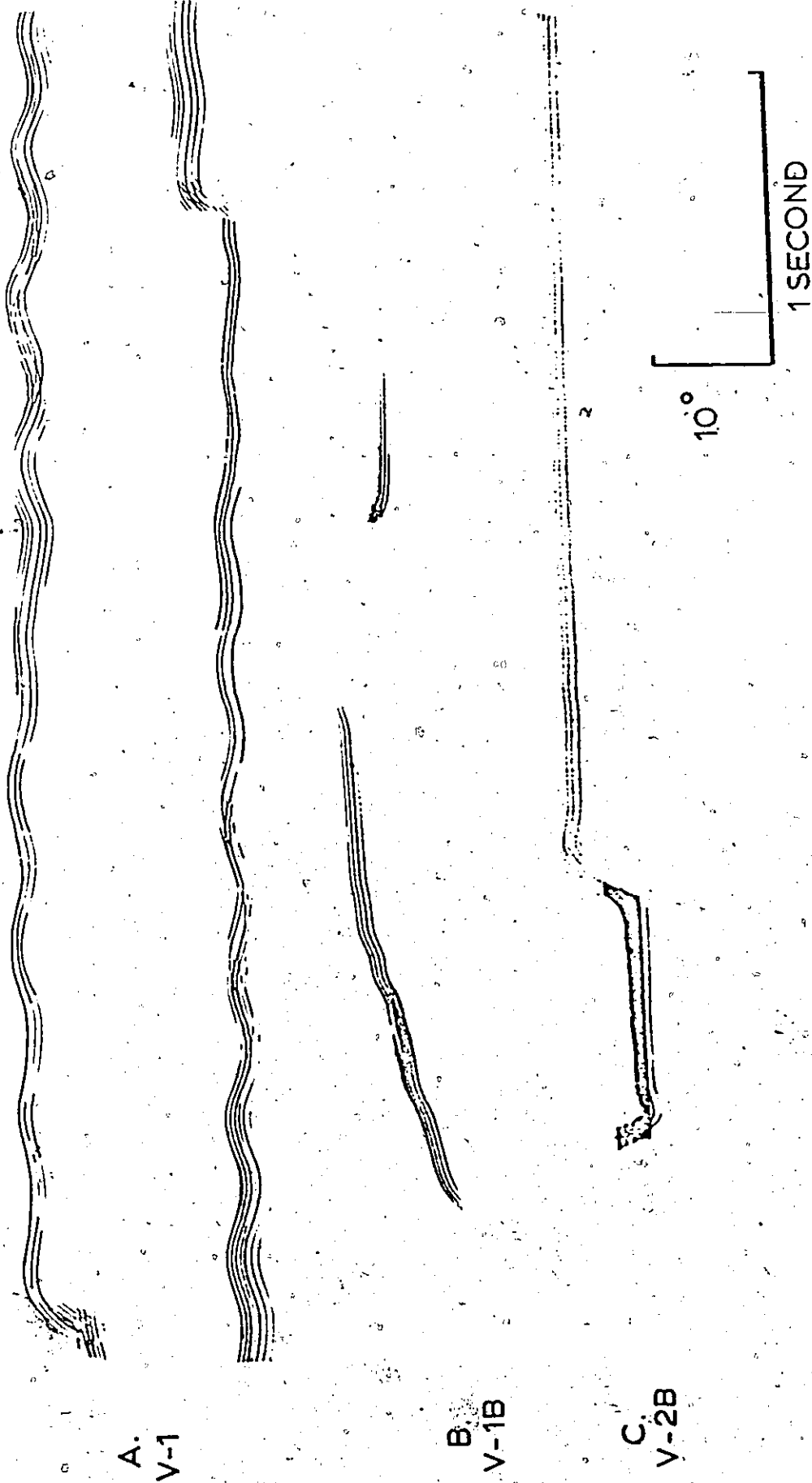
	Inter-flick interval	Mean drift velocity	Pendular eye movement	
			Frequency	Peak amplitude
Normal Human ¹	300-500 msec.	1 min.arc/sec.	---	---
Cat				
Normal ²	>1 sec.	30 min.arc/sec.	---	---
Vertical pattern reared	>1 sec.	1 degree/sec.	3-5 Hz	1.0 degree
Horizontal pattern reared	>1 sec.	1 degree/sec.	3-5 Hz	1.4 degrees
Oblique pattern reared	>1 sec.	30 min.arc/sec.	3-5 Hz	0.5 degrees

1 data from Ditchburn (1955)

2 data from Pritchard & Heron (1960)

Figure 7. Additional sample eye movements of restricted animals during visual fixation. A continuous record of a single fixation is shown in A.

FIXATION EYE MOVEMENTS OF RESTRICTED ANIMALS



A.
V-1

B.
V-1B

C.
V-2B



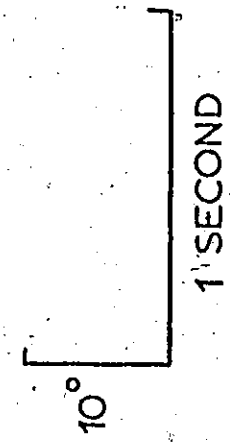
D.
Ob-1

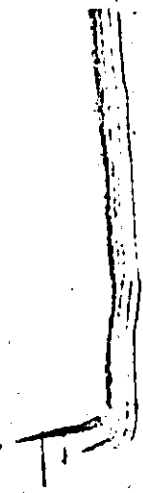


E.
Ob-2

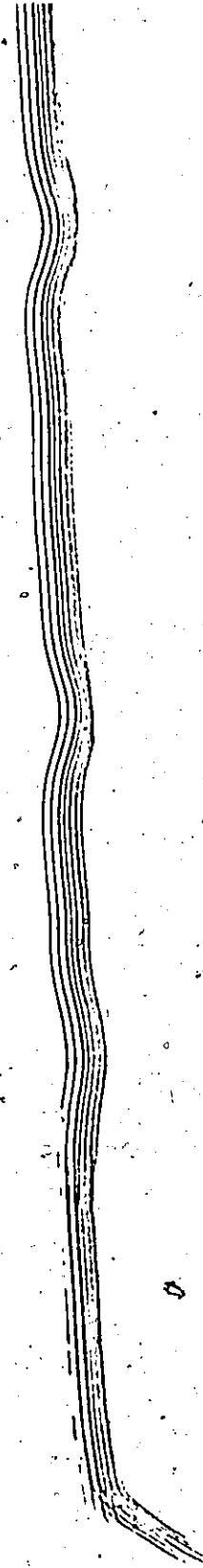


F.
Ob-2B

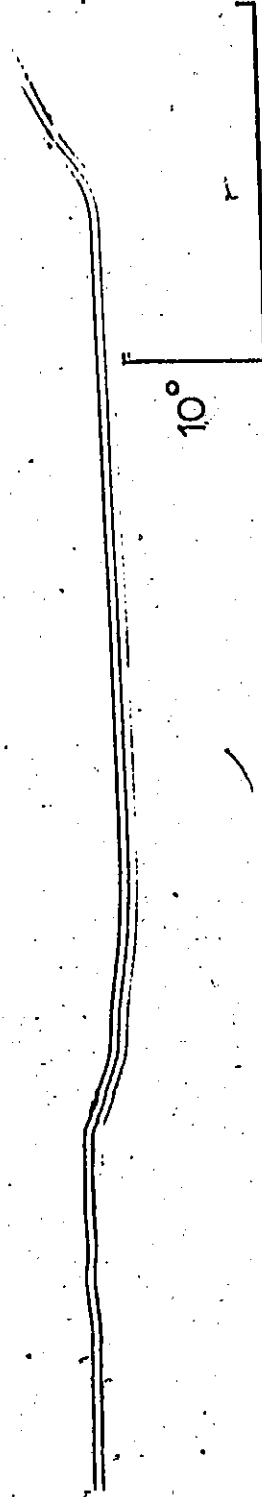




G.
Da-1.



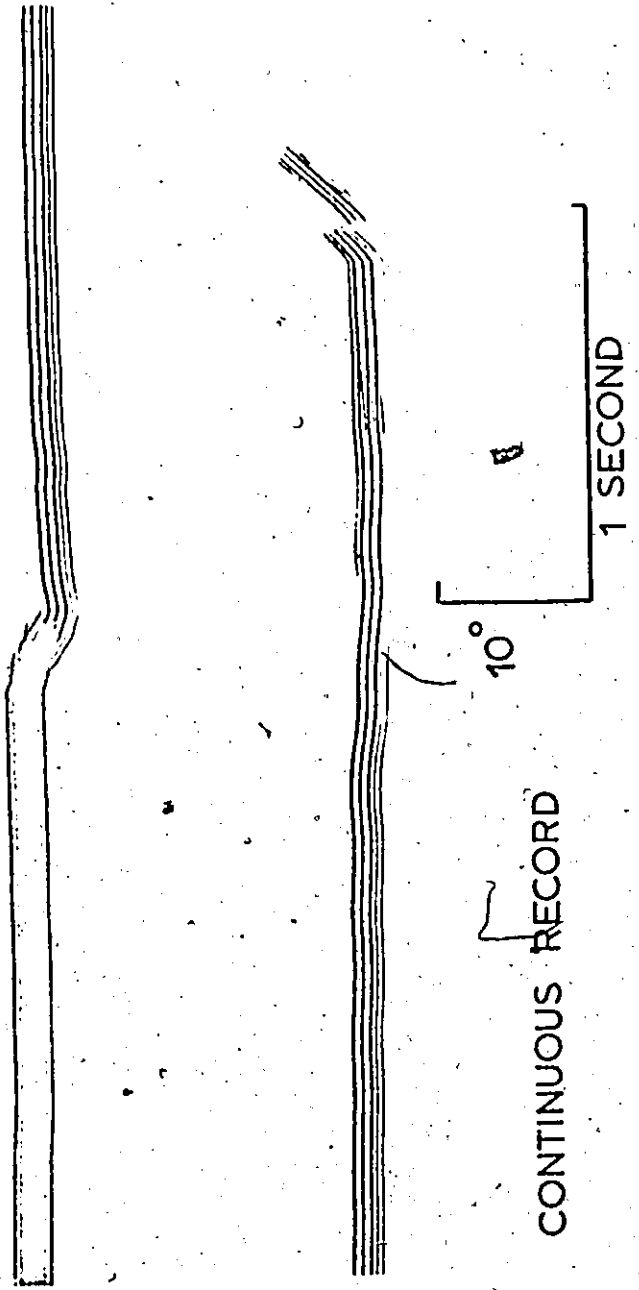
H.
Da-1



I.
UNRC

Figure 8. Effect of restraint on eye movements of animal H-1 during visual fixation. Large amplitude tremor movements could not be recorded in this animal with the optic lever technique, though they were clearly present when the animal was unrestrained. Electro-oculographic recordings from animal H-1 while unrestrained are shown in figure 9.

EFFECT OF RESTRAINT ON FIXATION EYE MOVEMENT IN ANIMAL H-1



CONTINUOUS RECORD

1. Binocular tremor

The relation between the tremor in the two eyes of the restricted animals was investigated electro-oculographically. Figure 9 shows the EOG of an animal actively exploring the environment in a lighted observation chamber. It can be seen that the pendular nystagmus is generally conjugate in the two eyes. Although both eyes tend to move in the same direction at the same time, arrow 1 indicates an instance in which this is not the case. Here the left eye runs out of phase with the right eye for approximately four cycles and then the two eyes resume in-phase operation. The in-phase operation of the two eyes occurs even following a disjunctive eye movement (arrow 2).

Samples of recorded EOG activity were subjected to cross correlation analysis on a PDP-8 computer. The cross-correlograms shown in Figure 10, confirm that there is a consistent positive correlation between the movements in the two eyes at time 0. The differences between the cross correlograms taken in the light and those taken in the dark are related to a greater number of large amplitude eye movements in the light.

2. Effect of input

In order to determine whether active interaction between the two eyes was necessary to maintain nystagmus, the amount of time that eye tremor occurred during a 5 minute period with and without an opaque occluder over one eye was recorded with the cat in an observation chamber, using a counterbalanced design. All animals had nearly continuous tremor activity in this situation. Thus, simultaneous patterned input to both eyes was not necessary to maintain nystagmus.

Figure 9. Electro-oculograms of pendular nystagmus in both eyes.

Recordings taken from chronically implanted electrodes in animal H01. Arrow 1 indicates a point on the record where movements in the left eye are out of phase with movements in the right eye. Arrow 2 indicates a disjunctive eye movement which does not disrupt the tremor relation between the eyes.

EYE TREMOR WITH LIGHTS ON

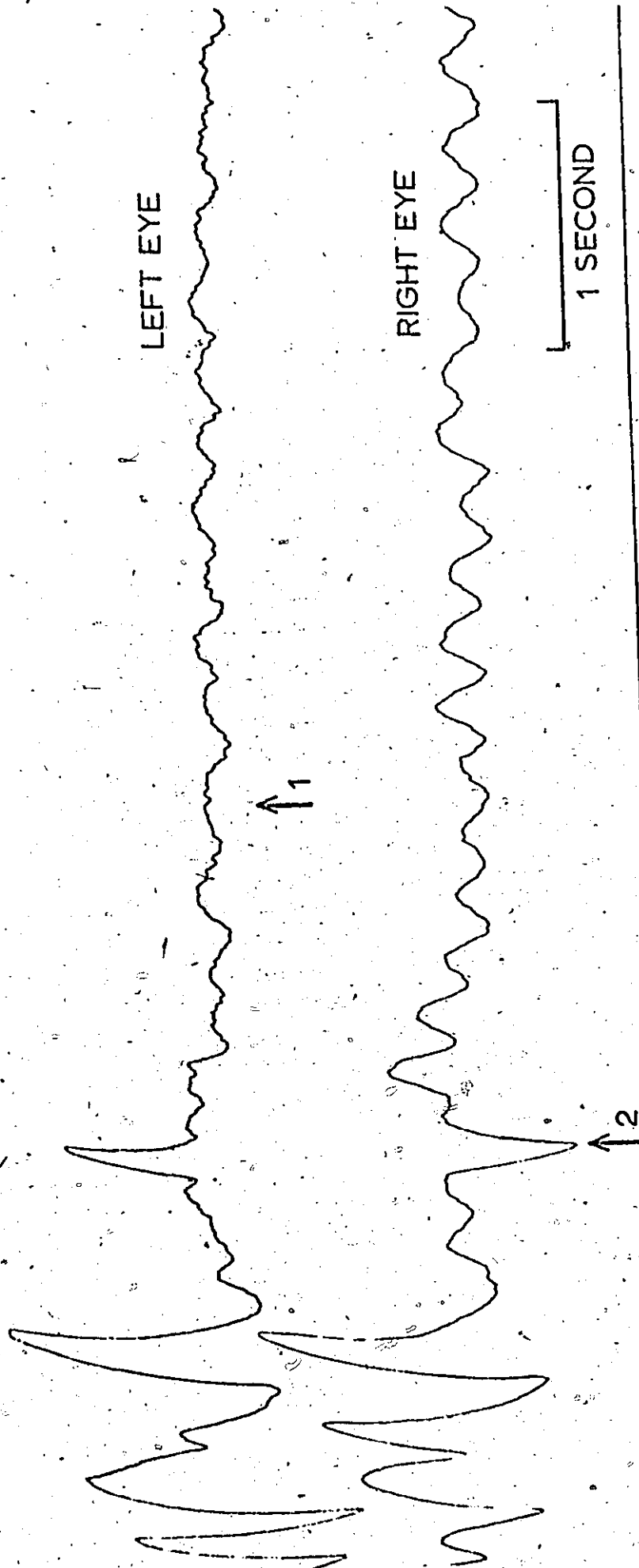


Figure 10. Interocular cross-correlation functions. Cross-correlations of right eye with respect to left eye compiled on PDP-8 computer using auto and cross-correlation package; Animal H-1; sampling rate: 20 msec.; A. lights on, B. lights off, C. cross-correlation of 5 Hz signal with itself for calibration.

CROSS - CORRELATION FUNCTIONS

RELATIVE CORRELATION

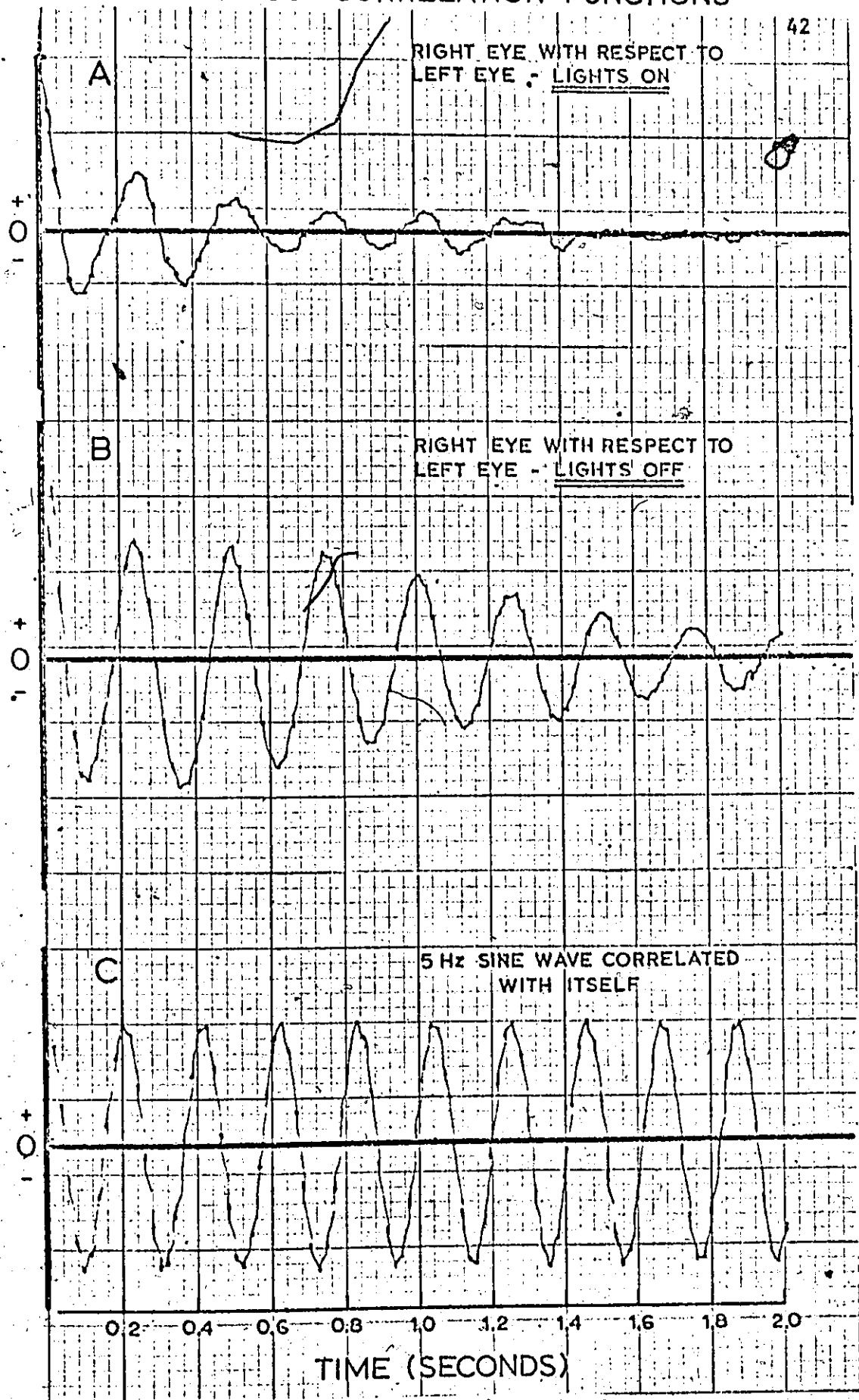


Figure 11 shows the EOG of an animal placed in the dark. Here, of course, there was no patterned input to either eye. It can be seen that under these circumstances tremor still persists. However, when the rate of bursts of nystagmus at least 5 cycles long was measured over 4 alternating 8 minute light and dark periods, it was found that the rate was much greater in the light (1.9/minute) than in the dark (0.7/minute).

It should be noted that nystagmus would almost invariably be evoked by noises such as hand claps (figure 12) or scratching on the box, whether the animal was in the light or in the dark. In the light it was observed that these noises tended to be followed by searching behavior. Further, it was found that in recordings from an animal with EOG electrodes, 88% of the instances of tremor occurred within a second of a saccadic movement of at least 10 degrees. Thus, periods of tremor were usually associated with active visual searching. This was seen both in EOG recordings and in observations of all animals with tremor.

B. Saccadic eye movements

The latency of saccadic eye movements was measured as follows. The cat was put in the restraining box and gold-plated insect pin electrodes were inserted subcutaneously temporal to each eye and held in place by adhesive tape. The electrodes were referred to each other, and the output was fed into an AC coupled oscillograph and recorded on magnetic tape.

An apparatus controlled by a Grass S8 multifunction stimulator produced a sequence of events (see figure 13) which was designed to induce the animal to fixate one light and then shift fixation to another. At the beginning of a trial, which was initiated by the experimenter only

Figure 11. Electro-oculograms in light and dark. Recordings taken
from chronically implanted electrodes in animal H-1.

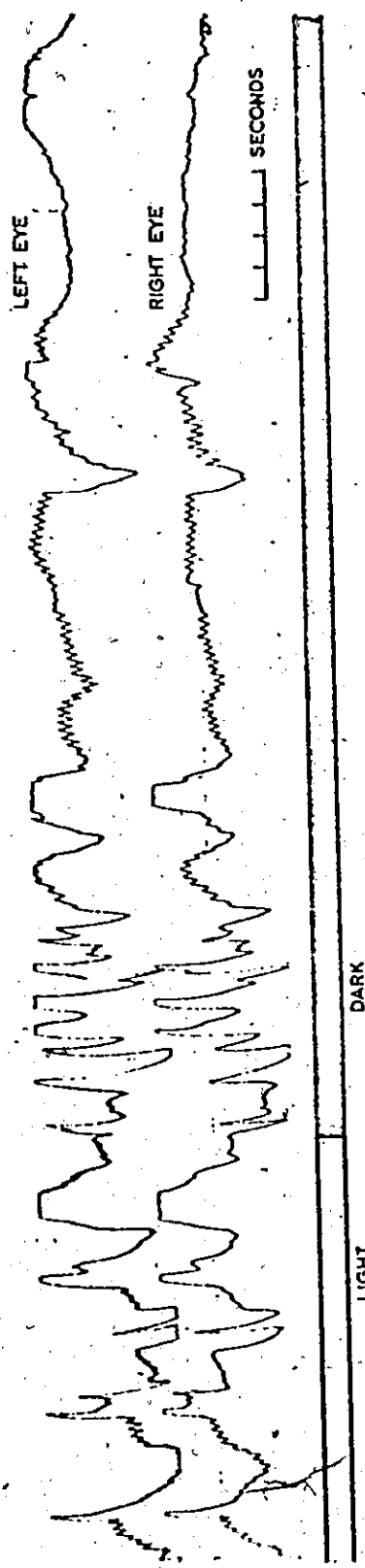


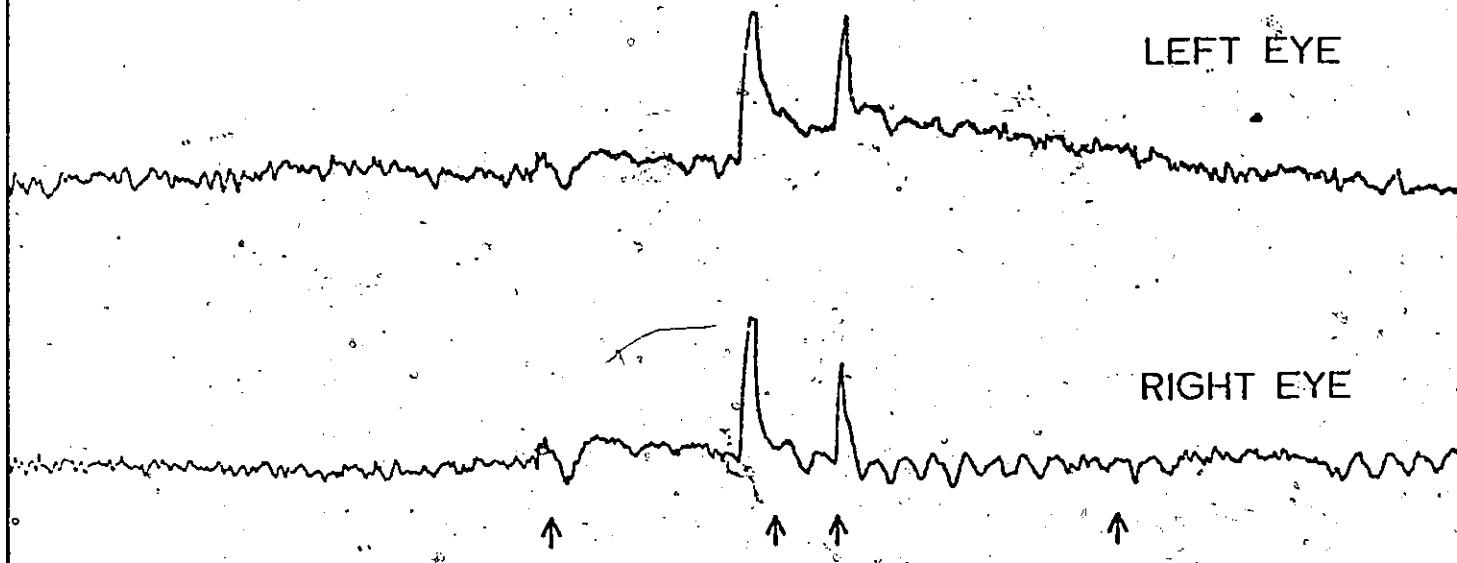
Figure 12. Effect of sudden noise on eye movements of a restricted animal. EOG recordings of animal H-1. Arrows indicate the occurrence of a hand clap or a knock on the door of the observation room.

EFFECT OF SUDDEN NOISE ON EYE MOVEMENTS

A. LIGHTS ON

LEFT EYE

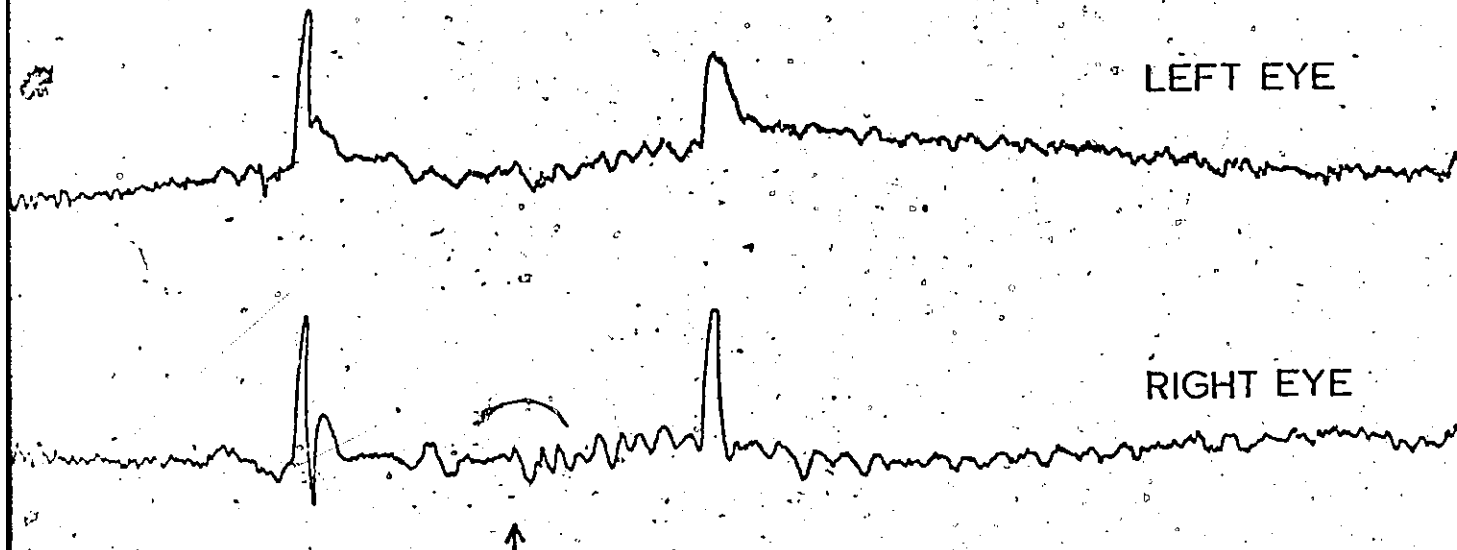
RIGHT EYE



B. LIGHTS OFF

LEFT EYE

RIGHT EYE

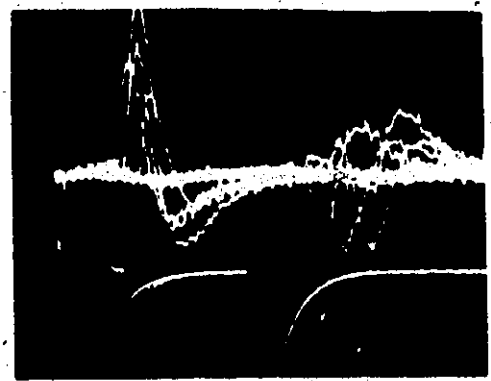


1 SECOND

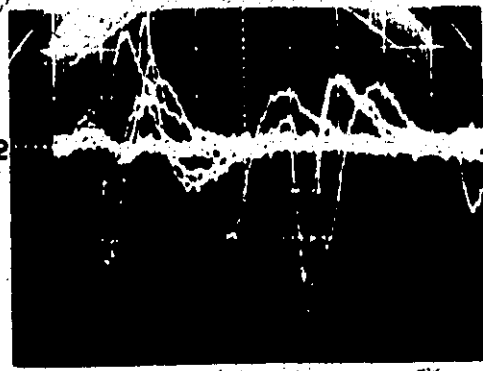
TIGHT
BINNING -

Figure 13. Typical EOG recordings of saccadic eye movements. Stimulus sequence indicated below records. Animals were restrained in a dark room facing the stimulus panel, the source of the tone was a small loudspeaker directly behind the left fixation light, and the separation between fixation lights (light emitting diodes) was 10°.

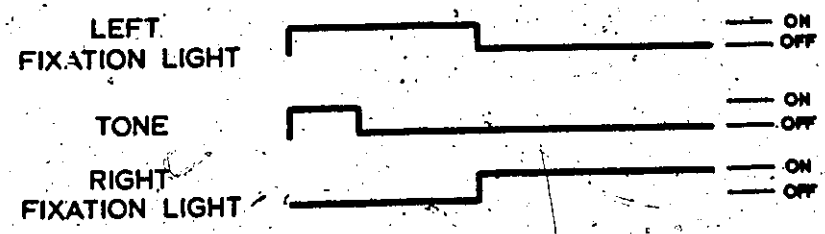
A. OBLIQUE -1



B. HORIZONTAL -2



200 msec.



when the monitored EOG record showed no large eye movements, a small light in an otherwise dark room appeared in front of the animal for half a second accompanied by a tone (varied from 100-10000 hz. to reduce habituation) lasting for a quarter of a second. When the first light went off a second light appeared 10° to the right. Although no animal run in this procedure responded on more than 50% of the trials, when responses occurred the latency was reliable and idiosyncratic.

In general, even though the specially reared animals had dramatic abnormalities of fixation, the range of saccadic latencies of six restricted animals (110-340 msec., see table 3), estimated from photographs of the EOG, were within the range of latencies of five normal cats (110-400 msec.). Two typical records from this experiment are shown in figure 13 which illustrates the consistency of response, especially to the light-tone onset.

C. Interocular alignment

After early visual restriction many of the animals were found to have abnormal interocular alignment as assessed by the light reflex technique described previously, and a procedure in which the horizontal distance between the optic disc centers was determined by directly observing the retinas in animals paralyzed with gallamine (Sherman, 1972). The latter procedure is described more fully in the single unit method section. Both procedures were used in all but three of the restricted animals. In these three animals (MO-1, RC-3, and V-1) only the light reflex technique was used.

The horizontal separation between the optic disc centers in the paralyzed state is shown in figure 14 where it can be seen that in all

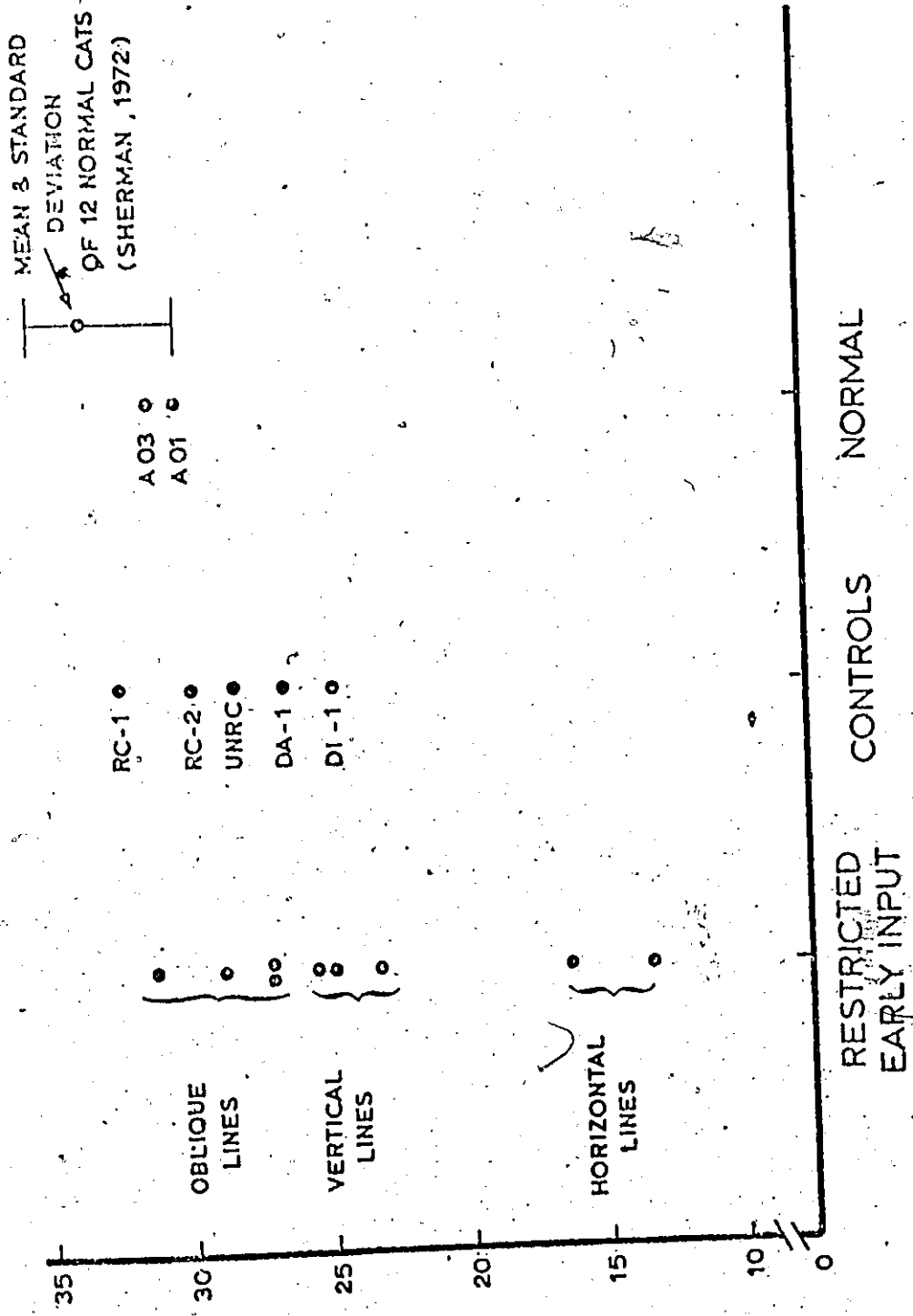
Table 3. Estimated saccadic latencies. Latency estimates made from EOG recordings of horizontal saccades for six restricted and five normally reared cats.

Table 3
Estimated Saccadic Latencies

Animals	Latency (Msec.)
<u>Restricted cats</u>	
H-1	340
H-2	180
V-1	200
V-2	240
O-1	250
O-2	110
<u>Normally reared cats</u>	
I09	280
D15	200
I11	400
I15	110
G07	300

Figure 14. Eye alignment in paralyzed state. Each point represents the distance between the projected optic disc center of a single paralyzed animal. Data from two normally reared adult animals are presented along with the mean and standard deviations of eye alignments in 12 normal cats measured by Sherman (1972).

DISTANCE BETWEEN OPTIC DISK CENTERS
IN PARALYZED STATE (DEGREES)



cases where eye deviation occurred, convergent rather than divergent squint was observed. The animals exposed to horizontal lines had the most extreme cases of convergent squint, while those reared with vertical stimulus patterns showed less deviation, but still, as a group, more than did those restricted to lines of 45° .

A point of particular interest about the data in figure 14 is that animals with abnormal interocular alignment maintained this condition while paralyzed.

For the three animals in which only the light reflex technique was used, no detectable eye deviation was observed in the two control animals, while animal V-1 had a marked convergent squint.

Single Unit Recordings.

Methods.

Fourteen restricted animals were prepared for single unit study. All surgical procedures were performed under Halothane anaesthesia. Following preparation, Halothane was discontinued and nitrous oxide anaesthesia (70% N₂O, 30% O₂) was begun. Animals were paralyzed to reduce eye movements with an intravenous injection of 40 mg. of gallamine (Flaxedil) and artificially respired at a rate and volume adjusted to the size of the animal. Paralysis was maintained by supplementary doses of gallamine (20 mg./hour). Rectal temperature was monitored and was thermostatically maintained at 37°C by a heating pad on which the animal was placed. Dehydration was reduced by the intravenous injection of a saline solution containing 5% glucose usually about 10 hours after initial paralysis. In no case was recording begun less than 2 hours after the cessation of Halothane anaesthesia.

After the recording, gallamine was terminated and prostigmine was injected intravenously to recover the animal. Three animals died before any unit activity could be recorded. One of these (V-1) died during initial induction with Halothane anaesthetic. This animal was one of the original group which had been in a normal laboratory environment for nearly two years. V-1 like the other specially reared animals showed the emotional withdrawal characteristic of animals deprived of stimulation during early life (Thompson & Heron, 1953). Like the other deprived animals in this series, V-1 froze and held a passive fixed position during anaesthesia induction. This is a pattern very unlike the behaviour of normal cats who often struggle violently at this stage

of preparation. V-1 stopped moving and eventually stopped breathing during induction. Once this pattern was noted in V-1 who was an early animal in the series, the same pattern was observed in the other deprived animals during initial anaesthesia, and with special precaution it was possible to prevent further mishap. A similar relation between sedation threshold and emotionality has been found in human subjects (Claridge, 1967). The two other animals which died before neural information could be obtained (RC-1 and RC-2) were the youngest animals in the series and both died for unknown reasons after the induction of paralysis.

Preparation proceeded after an endotracheal tube coated with 5% Xylocaine ointment was inserted and all pressure points had been infiltrated with long-acting procaine in oil (Proctocaine). The animal was placed in a head holding apparatus (Hamilton Research Instruments) which allowed unrestricted visual stimulation, and an intravenous cannula was inserted in the left saphenous vein. Following a mid-line scalp incision, the skin and fascia were retracted, the skull cleaned of all tissue, and a hole approximately 2 mm. in diameter was drilled through the skull above each lateral gyrus. The holes were filled with bone wax, and small jewellers screws with soldered connectors to record cortical EEG were installed in the skull as close to the holes as possible. Gold-plated insect pins with soldered connectors were inserted subcutaneously in each forepaw to record heart rate.

The eyes were prepared with drops of phenylephrine hydrochloride to retract the nictitating membranes, and a solution of atropine and physiological saline (.4 mg/cc.) to dilate the pupils. Optically neutral contact lenses were placed on the eyes to prevent drying of the corneas.

Neural activity picked up by a microelectrode was fed into a Grass Model P15 pre-amplifier with band pass set from 100 Hz to 3 KHz. The head clamp which was in contact with the inside of the animals mouth served as the indifferent electrode. Activity was monitored on one beam of a Tectronix 502A oscilloscope which was in line with a Schmitt trigger and loud speaker. Action potentials were recorded on an Ampex SP-300 7 channel tape recorder. A second oscilloscope was used to monitor the recorded signal. In addition, a stimulus marker was displayed on an oscilloscope and recorded on the tape. EEG activity was also fed into a Grass P15 pre-amplifier and displayed on an oscilloscope as well as being recorded. Heart activity was amplified by another Grass P15 and displayed on an oscilloscope as well as being monitored by ear with a second Schmitt trigger and loud speaker.

Epoxy coated tungsten microelectrodes (Hamilton Research Instruments) were used with a tip size of about three microns. The electrodes were held in a hydraulic microdrive (Trent-Wells) suspended rigidly above one of the holes in the skull. The position of the microdrive could be modified to allow penetration at different angles, and in order to sample activity from many columns all penetrations were made obliquely to the surface of the cortex.

Stimulus patterns were presented on a rear projection screen situated approximately 40 cm. in front of the cats' eyes. Ancillary achromatic lenses (usually 5 to 6 diopters) brought the image on the screen into focus on the retina. A beam splitter was used to observe the retina while focusing the image. The cats head was placed so that the position of the area centralis (Bishop, Kozak & Vakkur, 1962)

corresponded approximately to the center of the stimulus screen. The beam splitter was used to plot the projections of the optic discs on the rear projection screen so as to provide landmarks for determining the retinal position of stimuli and to provide a measure of ocular alignment. The locations of the optic discs were checked during the course of each experiment.

Patterns were presented by a modified Leitz slide projector (Prado Universal). A mirror mounted on a galvanometer coil was fixed in front of the projector lens and a series of prisms fixed rigidly to the mirror assembly, so that stimulus patterns could be rotated around the central axis and oscillated at a variety of frequencies. The galvanometer was driven by a multifunction stimulus generator (Krohnhite Model 420C). The luminance of the light side of any stimulus pattern was approximately 15 millilamberts, and the dark side luminance was approximately 0.1 millilamberts.

When searching for a unit, a herringbone search pattern containing many lines and edges was driven in a square wave motion at 3 Hz, because edges moving at 3 Hz have been found to be a most effective stimulus for neurons in the visual cerebral cortex (Hubel & Wiesel, 1962; Burns, Heron & Pritchard, 1962). In addition to this search pattern a variety of hand-held cardboard edges was often used while searching for units and while determining receptive field characteristics.

The main objective of the present study was to determine the effects of experience on the stimulus orientation of maximum activity (SOMA) of units in the visual cerebral cortex, so clusters of cells as well as single units were recorded since it was found that when clusters were encountered all

units observed appeared to be sensitive to the same orientation of stimulus pattern. Examination of the records indicated that a conservative estimate of the number of units per cluster was five.

The SOMA of cortical units was determined by the use of hand-held stimuli and a black-white square wave grating of approximately 2 lines per degree moved by a square wave signal at 3 Hz with an amplitude of 1.5°. The orientation of the grating stimulus was adjusted so that the maximum cell response was obtained. The use of the grating stimulus pattern allowed the SOMA to be determined before the exact location of the receptive field was specified. The exact location of a unit's receptive field was a relatively low priority in this study, though many fields were plotted directly on the rear projection screen with a wax pencil after other information was obtained. At the end of each experiment a polaroid photograph of the rear projection screen was taken to record field positions as well as the separation of the optic discs.

Ocular dominance was assessed by occluding first one eye and then the other and determining the relative contribution of each eye to the response. Only three categories of ocular dominance were used. If cells fired when either the ipsilateral or contralateral eye was stimulated they were classed as binocular, otherwise the activity was categorized as ipsilateral or contralateral. Where activity was encountered which demonstrated no orientation specificity, was monocularly controlled, and which responded to diffuse flashes of light, that activity was classed as probably of fibre origin. Occasionally activity was encountered which could not be affected at all by visual stimulation. This activity was categorized as not following if it occurred in the vicinity of activity

which did follow visual stimuli.

Results

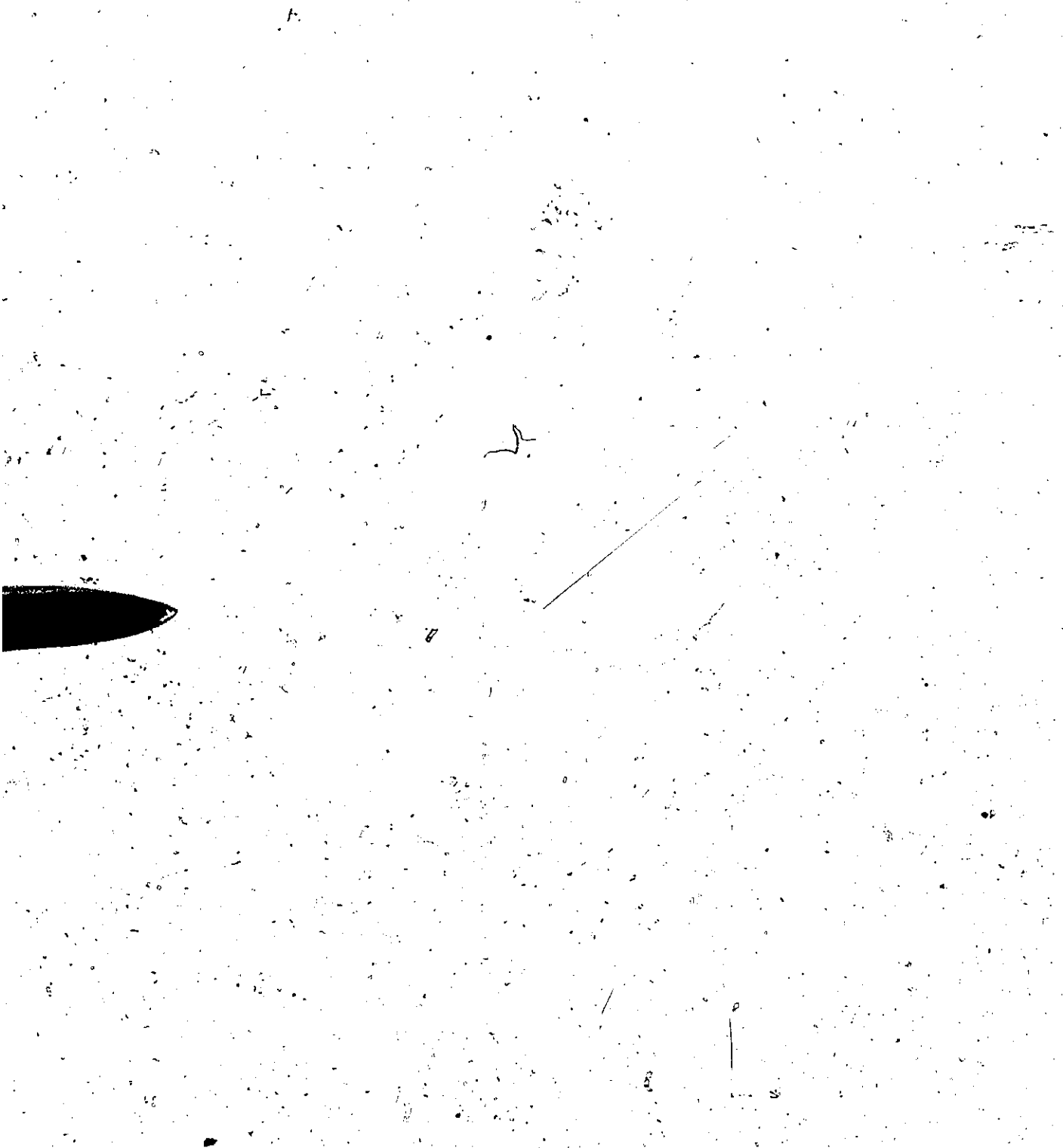
Activity was recorded from a total of 140 single units and 79 cell clusters. 8 of the clusters and 9 of the individual units were considered to be fibres of geniculate origin (see Appendix).

1. Orientation specificity

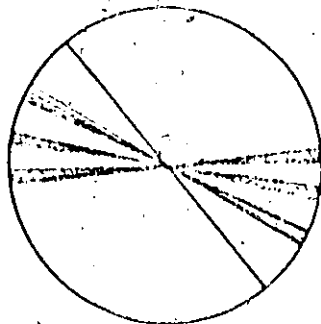
The stimulus orientations of maximum activity (SOMAs) of all cortical units recorded in each animal are diagrammed in Figure 15. Figure 15A and B show that the orientation specificities of most of the units encountered in the animals reared in horizontal or vertical visual environments matched the orientation of the stimulus patterns to which the kitten was exposed. This is true even though recordings from three of these animals (H-1, H-2, and V-2) were made after they had been housed for almost two years in a normal laboratory environment following the early restricted rearing environment. Of particular interest in Figure 15A is that for animal H-2, although about 80% of the cells responded optimally to stimuli oriented within 20° of the horizontal meridian, those units which did not respond optimally to horizontal stimuli generally responded optimally to vertical stimuli. The picture is least clear for V-2. This animal was especially active when placed in the rearing tube and occasionally managed to remove the collar which prevented sight of its limbs during the rearing period. However, for V-2, as for the other animals reared with early visual experience limited to vertical or horizontal lines, the SOMA anisotropy of cortical units is significant (Chi-squared test; $p < .05$ for V-2, $p < .01$ for other animals).

Figure 15C shows the SOMAs of cells encountered in the four animals reared with oblique patterns. The SOMAs of units in these

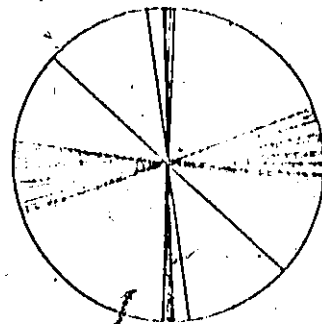
Figure 15. Stimulus orientations of maximum activity (SOMAs) for cells in the visual cerebral cortex of experimental and normal animals. Each diagonal indicates the SOMA for a single cell.



A. HORIZONTAL VISUAL EXPERIENCE

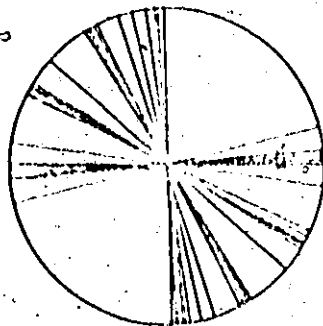


HORIZONTAL - 1

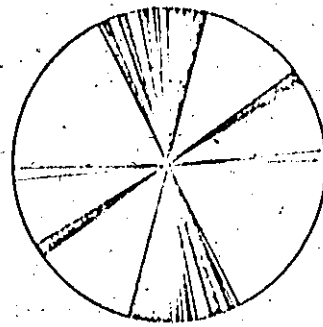


HORIZONTAL - 2

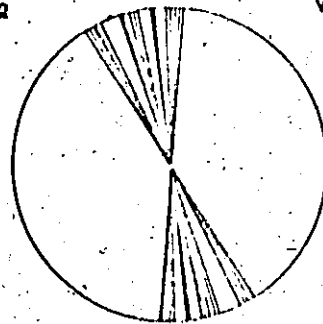
B. VERTICAL VISUAL EXPERIENCE



VERTICAL - 2



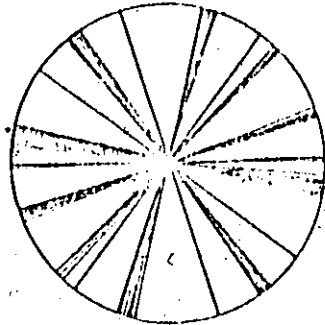
VERTICAL - 10



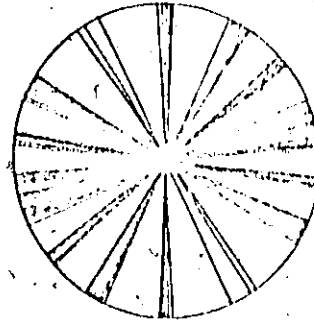
VERTICAL - 20

C.

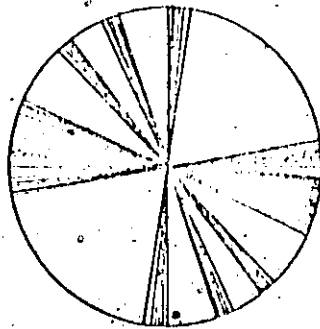
OBLIQUE VISUAL EXPERIENCE



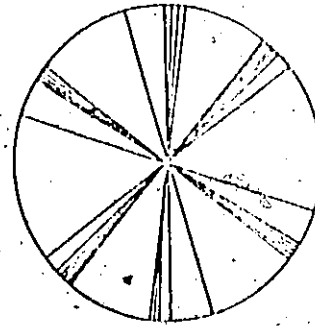
OBLIQUE - 1



OBLIQUE - 2



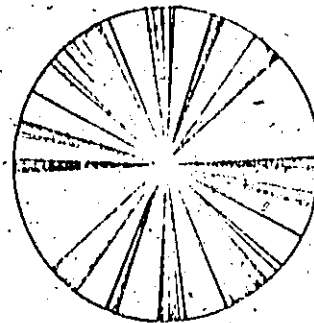
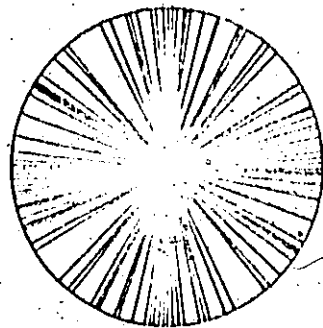
OBLIQUE - 1B



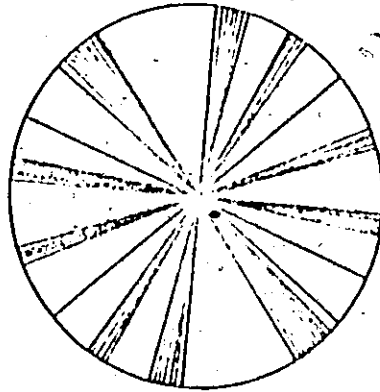
OBLIQUE - 2B

D. NORMALLY REARED
ADULTS (HOEPPNER '71)

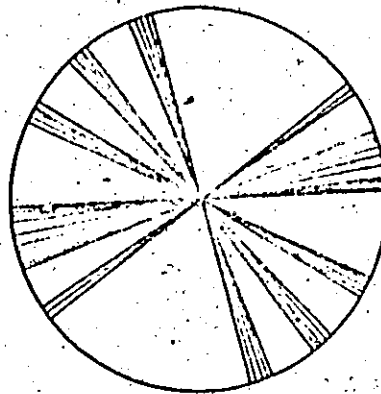
E. UNRESTRICTED
CONTROL



F. DARK REARED



G. DIFFUSE REARED —
NO EARLY PATTERNED
EXPERIENCE

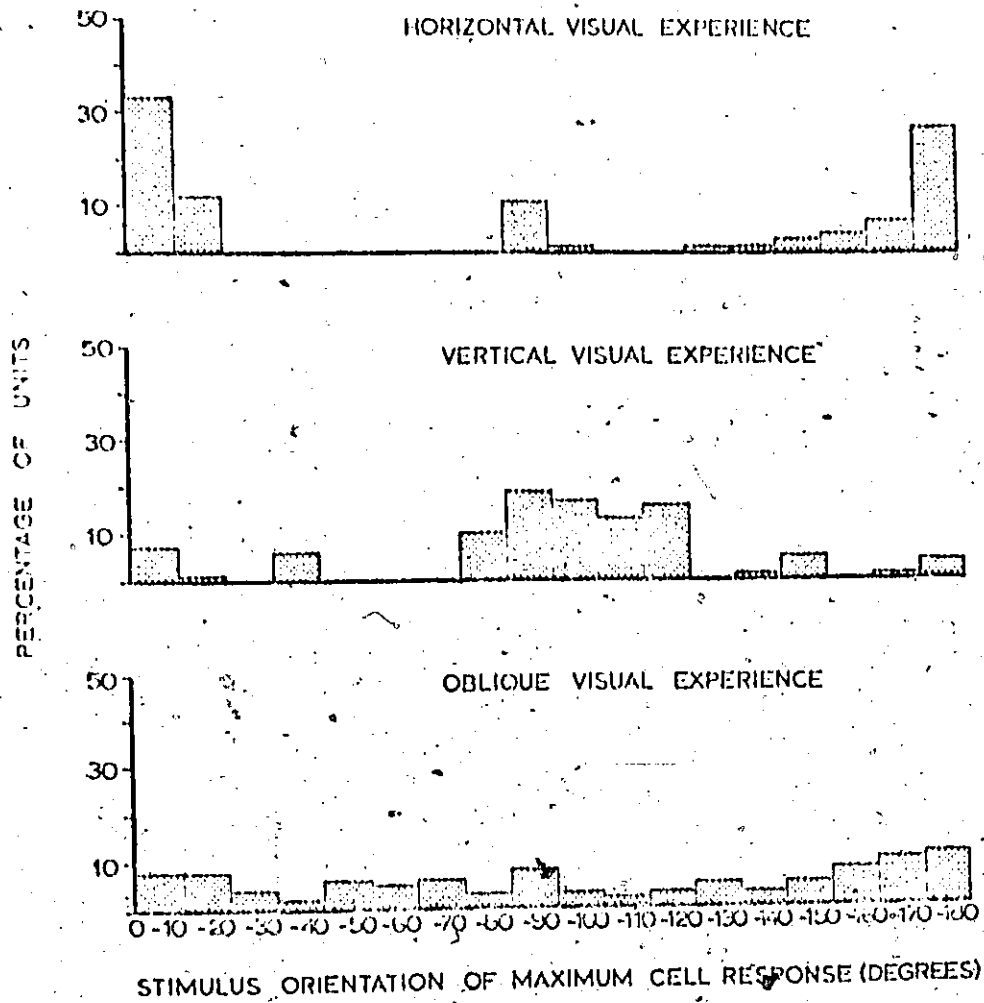


animals differ from the SOMAs of units in animals reared with either vertical or horizontal experience in that the experienced orientation is not most commonly encountered. Comparison with Figure 15D which shows the distribution of stimulus orientations of maximum activity of 56 neurons recorded in 31 normally reared cats by Hoepfner (1971) shows that the distribution of SOMAs of units in animals reared with oblique visual experience approximates the distribution found in normally reared cats, except in the case of animal 0-1B. The distributions in normally reared cats, and in animals 0-1, 0-2, and 0-2B are not significantly different from what would be expected if all orientations were equally represented (chi-square). 0-1B has a significant anisotropy ($p < .01$) but the most common orientation is horizontal, not oblique. It should be pointed out that on termination of restricted visual experience this cat was found to have the blue iris and red retina characteristic of albino animals. Its litter mate had no overt signs of albinism.

Figure 15E shows the distribution of SOMAs of units encountered in the unrestricted control animal (UNRC). A chi-square test showed that this distribution was not significantly different from normal. Animal UNRC spent the same amount of time in the dark as its litter mates but viewed a normal visual environment while the others viewed a restricted visual environment. The distributions of SOMAs of units in the animal reared in the dark and the animal given visual experience in an unpatterned restricting tube are shown in Figures 15F and G respectively. The dark reared animal had no significant anisotropy, but the animal reared with diffuse visual experience did ($p < .05$).

Figure 16 summarizes the main findings with histograms of the

Figure 16. Histogram showing the percentage of cells which respond best to a stimulus orientation within the 10° ranges indicated. Each histogram was compiled by combining the relevant data displayed in figure 15.



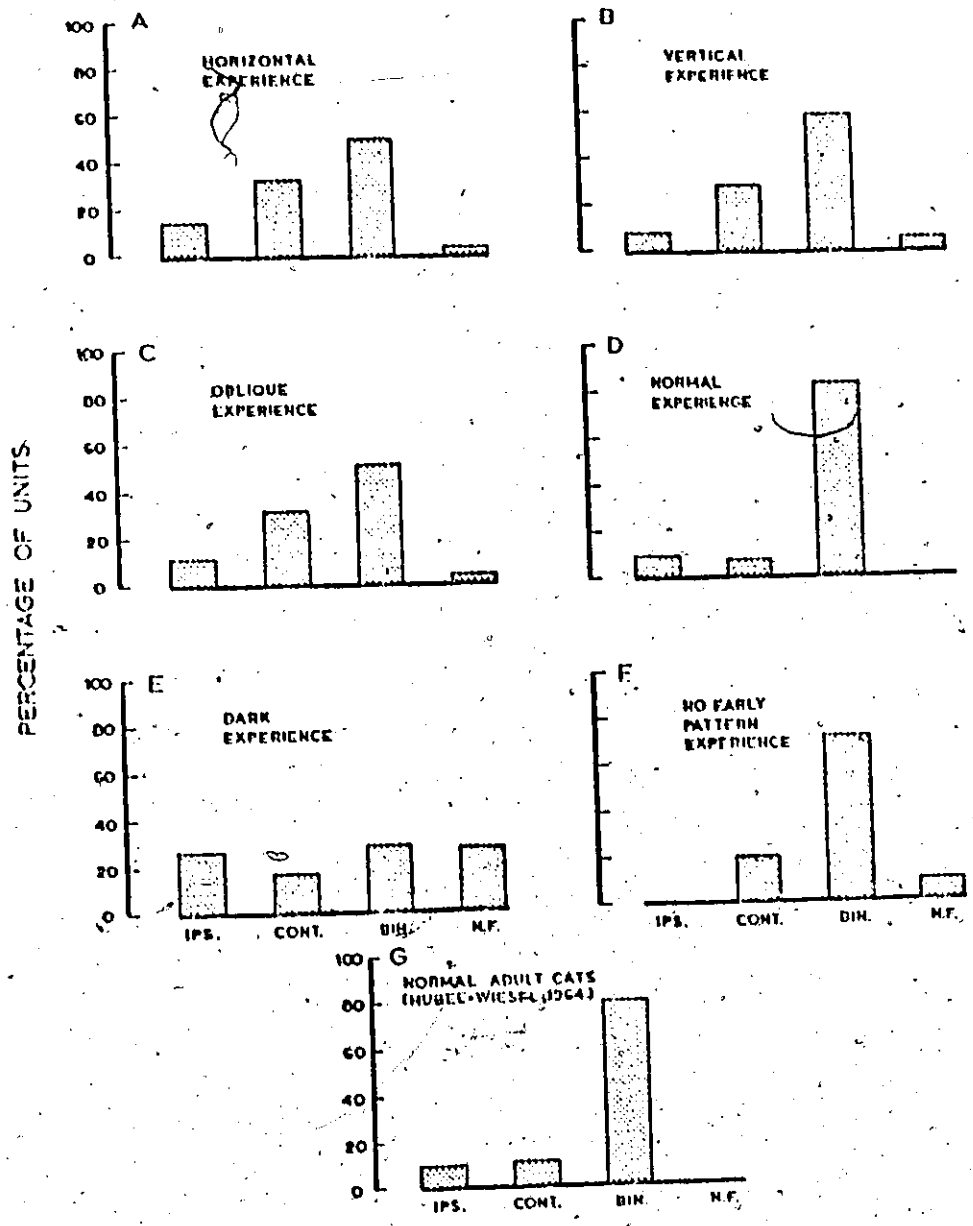
percentage of units having particular SOMAs for all animals in each of the three major rearing conditions. The SOMAs of units in animals with vertical or horizontal visual experience are clustered around the experienced orientation. In animals with oblique visual experience on the other hand all orientations are approximately equally represented in the distribution of stimulus orientations of maximum cell response.

II. Ocular dominance

The binocular function of units encountered in the restricted animals was abnormal. There were relatively fewer cells which could be driven by stimulating either the ipsilateral or the contralateral eye. even those units with demonstrable binocular input were unusual in that there often did not seem to be discrete receptive fields. That is, while in the normal cat corresponding discrete receptive fields can be found for each eye, in the restricted animals, although the cells could be driven by oscillating the grating stimulus pattern, plotting the field for one or both eyes often proved to be impossible. Further, one eye usually dominated these binocular units; the responses to stimulation of one eye were much stronger than the responses to stimulation of the other. Finally, on at least 6 occasions two adjacent cells were found which were monocularly controlled though one was responsive only to stimulation of the contralateral eye, while the other responded only to stimulation of the ipsilateral eye.

Figure 17 shows the percentage of cells which could be driven by stimulation of the ipsilateral or contralateral eye alone, and the percentage responsive to stimulation of either eye. Also, the percentage of unresponsive cells is indicated. In compiling this figure individual

Figure 17. Ocular dominance patterns of units recorded in restricted and normal animals. I.P.S. - responds only to stimulation of ipsilateral eye; CONT. - responds only to stimulation of contralateral eye; BIN. - responds to stimulation of either ipsilateral or contralateral eye; N.F. - no following to any visual stimulation.



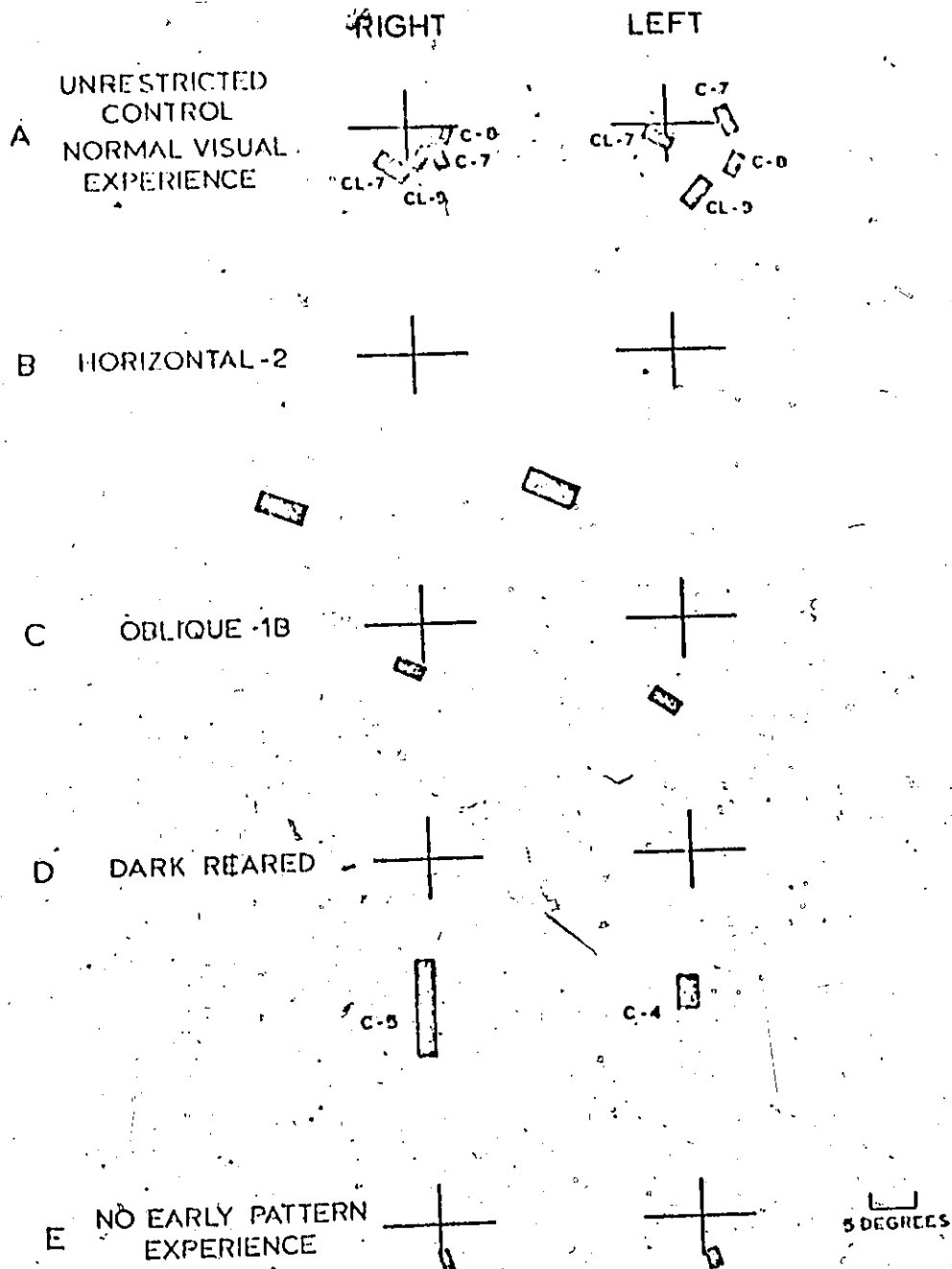
units and clusters of units were combined because the ocular dominance distributions were similar. A cluster was categorized as binocular if there was any response to stimulation of the ipsilateral and to stimulation of the contralateral eye. Thus the histograms tend to overestimate the number of binocular units since neighbouring monocular units may receive input from different eyes. Despite this, the percentage of units with binocular visual input in the horizontal, vertical and obliquely reared animals (50%, 50% & 52% respectively) is less than the percentage of binocular units encountered in the unrestricted control animal (83%). Figure 17G shows the distribution of 223 cells recorded from a series of normally reared adult animals by Hubel and Wiesel (1964), where 80% of the units showed binocular interaction.

Finally, it should be noted that in all of the restricted animals there was a small percentage of units which were unresponsive to visual stimulation. This was most apparent in the cat reared in the dark where 27% of the cells behaved in this way.

III. Binocular correspondence

In an animal with squint a stimulus object does not form images on corresponding points of the two retinas. It would obviously be of interest to know whether receptive fields of binocular units in these animals were normal. Nine examples are shown in Figure 18 along with some binocular fields of units recorded from the unrestricted control animal which had normal visual experience. This figure was compiled from the photographs of field position taken at the end of each experiment, the location of the area centralis being estimated with the method of Bishop, Kozak & Vakkur (1962). The estimated center of the area

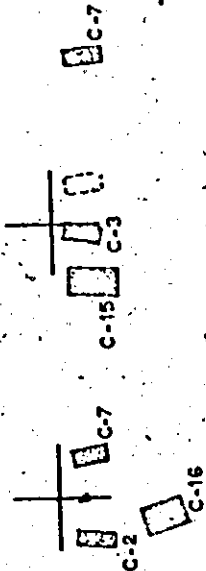
Figure 18. Receptive field positions of binocular cortical units
in restricted animals. The position of the area centralis in each
eye (estimated by the method of Bishop, Kozak, and Vakkur, 1962) is
indicated by the cross bars. Where receptive fields were found to
be at non-corresponding positions in the two eyes (F, G, and H),
the corresponding position in the left eye is indicated by a
dashed outline.



RIGHT

LEFT

F VERTICAL-1B



G HORIZONTAL-1



H OBLIQUE-2



C-12



5 DEGREES



centralis in each retina is indicated by the cross bar in each section of Figure 18.

Figure 18A shows the field positions of two cells and two clusters recorded from the unrestricted control animal. This example is given to indicate the probable degree of error of measurement, since this control animal had no observable squint and had normal eye movements and unit responses. Figure 18B, C, D and E show examples of cells (recorded in animals with squint) whose receptive fields fall on corresponding points of the two retinas. The cell recorded in animal H-2 (Figure 18B) is perhaps most striking, since this animal had a convergent squint of 11° and had been in a normal environment for almost two years after restriction. The example of Figure 18D also merits special mention as this was a case where two cells were recorded on the same record but one was responsive only to stimulation of the ipsilateral eye, the other only to stimulation of the contralateral eye. It can be seen that the fields of these cells fall on approximately corresponding points on the two retina, though here again the animal had a convergent squint, in this case estimated to be about 3° .

Figure 18F, G, and H show examples of binocular interaction in which the binocular receptive fields fall on noncorresponding positions on the two retinas. Figure 18F showing cells recorded in cat V-1B shows both types of arrangement in an animal which had a convergent squint of 8° . Cells 2 and 3 recorded at the same electrode position have receptive fields with corresponding positions on the two retinas as do cells 15 and 16 which were recorded within 50 microns of each other. In the case of cell 7 however, the left field position is approximately 11° lateral to

the corresponding position, thus the fields would have been approximately aligned on a single visual stimulus when the eyes were in the deviated position. A similar arrangement holds for the cell recorded in H-1 (Figure 18G) where the fields are displaced by about fifteen degrees, the estimated convergent squint being about 18° . In animal O-2 (Figure 18H) where two cells were recorded from the same electrode position the shift is less than the previous two examples (about 7°) and so is the estimated convergent squint (about 4°).

Discussion

The major contribution of the present study is that it has described in some detail the effects of early visual experience on visual alignment and eye movements. Further, this study has shown that limiting visual experience to horizontal or vertical patterns has a greater effect than limiting it to patterns which are oriented at 45°.

This effect of oblique early pattern experience is also observed when the receptive fields of units in the visual cortex are examined. While, like others (Blakemore and Cooper, 1970, 1971; Hirsch and Spinelli, 1970, 1971; Spinelli, et al., 1972; Pettigrew et al., 1973) we found that in animals reared with vertical or horizontal patterns the stimulus orientations of maximum activity for most cortical cells corresponded to the rearing condition, we discovered with some surprise that in animals reared with oblique patterns, the distribution of SOMAs of cortical cells sampled was similar to that observed in normally reared cats.

This result questions previous interpretations of how the early visual environment affects the nervous system (Pettigrew and Freeman, 1973; Van Sluyters and Blakemore, 1973). It should be remembered from the introduction that previous authors have implied that the developing visual system is almost infinitely plastic, that exposure to specific stimulus patterns produces a specific modification of the visual system. That is, exposure to vertical lines produces cells with a vertical SOMA and field shape, exposure to horizontal patterns shifts these measures toward horizontal, and so on. The present experiment emphasizes that the effect of early visual experience depends not only on the particular stimulus patterns used, but also on the structural organization of the

visual system.

As shown in the introduction, there is evidence suggesting that the visual system is arranged in terms of vertical and horizontal coordinate systems, and that these coordinates are specified separately in visual development. The finding that early exposure to stimulus patterns with vertical or horizontal orientations has effects different from exposure to patterns with an orientation of 45° is consistent with the anatomical analysis outlined above.

The fact that certain types of early visual input produce an approximately normal distribution of cortical cell SOMAs, while other types of early input produce a distribution skewed toward the experienced orientation, suggests that the development of a normal complement of stimulus orientation sensitive units depends on certain minimal requirements of input being met. The developing visual system can be seen not as being totally plastic and easily modified, but rather as containing within itself the rules of its own organization. The system does in a sense incorporate the organization of the environment within its structure, but this transformation of environmental order into order within the nervous system seems to occur within a relatively rigid framework. While the rules of this transformation cannot yet be rigorously specified, it can be concluded from the present work that early visual information organized along only vertical or only horizontal coordinates of the visual field is inadequate to produce a normal visual system.

If one assumes that normal visual development involves some early combination of vertical and horizontal input, then there are at least three possible mechanisms by which animals reared with oblique

line input could develop more normal visual function than animals reared with vertical or horizontal line input. Since the head was free to move in the restricted rearing situation used here, animals could have obtained an effective combination of vertical and horizontal input by head rotations. Alternatively, oblique input might produce normal function by simultaneously stimulating vertical and horizontal coordinate systems, and preventing a competitive imbalance between these systems. A third possibility, really a variant of the second, is that the relevant parameter is the dual activation of horizontal and vertical eye movement systems which are triggered by specific visual input. Clearly much research is needed to sort out these possibilities.

The percentage of binocularly activated single cells recorded from animals reared with restricted input was found to be less than normal in the present study. This result differs from previously published work in the area. Blakemore & Cooper (1970, 1971) report an approximately normal percentage of binocularly activated units in animals reared with either only vertical or only horizontal visual input, in a procedure very similar to the one used here. While it is possible that the differences between the percentage of binocular units encountered in the present study and the work of Blakemore & Cooper are due to sampling errors (their work involved only two animals), they also report that the binocular units recorded were normal in "almost every way". This was not the experience of the present investigator; receptive fields of binocular units were found to be difficult to localize and the amount of control exerted by

one eye was often very much greater than that exerted by the other eye. That is, though the cell would respond to stimulation of either eye, usually the response to one eye was strong, while to the other it was weak. Further, six neighboring unit pairs were encountered with each unit in the pair receiving exclusive input from one eye, though both eyes were represented in each pair of units. This organization can be interpreted as the result of a tendency towards segregation of input into ocular dominance columns, a pattern which is not apparent in normal cats but which becomes salient in kittens reared with artificial squint (Hubel and Wiesel, 1965). The study confirms the fact (Blakemore & Cooper, 1970, 1971) that animals raised with limited orientation experience develop binocularly activated units, but it calls into question the statement that these binocular units are essentially normal.

Why the results of the present study with regard to binocular activity differ from Blakemore and Cooper is not clear. One obvious possibility is that the difference exists because the animals in the two experiments had different post-restriction experience. Blakemore and Cooper tested their kittens 2 1/2 months after restriction, but kept them in the dark for this period (though the animals spent several hours per week under conditions in which they could be observed). The present cats were kept in normal laboratory conditions for periods of 4 months or 2 years before electrophysiological recordings were made. The argument here is that keeping the animal in a normal environment after restriction may result in reduced binocular activity.

The work of Hirsch and Spinelli (1970, 1971) and Spinelli et al. (1972) provides information about the effects of normal experience in

animals who have had restricted early input. Hirsch and Spinelli raised cats with visual experience restricted to stimuli mounted in goggles which were fixed to the animals' head. The result of this procedure was that animals were raised with entirely non-corresponding visual experience, so that it is not surprising that no binocularly activated cortical units were initially encountered in these animals. However, Spinelli et al. report that in follow-up testing of the original animals, 53% of the units encountered received binocular input after a maximum of 19 months in a normal environment. This finding has been generally confirmed by Pettigrew et al. (1973) who recorded cells from one of the initial Hirsch and Spinelli animals. Thus, reports have differed with regard to the level of binocular unit activity encountered in animals reared with restricted early input: Blakemore and Cooper (1970, 1971) found normal binocular activity in animals that had little normal experience, in the present study abnormal binocular activity was found in animals that had varying amounts of normal visual experience, and in animals which had no binocular activity following restricted visual experience it has been found (Spinelli, et al., 1972; Pettigrew, et al., 1973) that normal visual experience results in an increase in binocular activity.

The results of a recent elegant experiment by Van Sluyters & Blakemore (1973a) shed some light on these complexities. They set out to investigate an apparent paradox. Animals raised with artificial squint produced by cutting the medial rectus muscle of one eye (Hubel & Wiesel, 1965) have no binocularly activated units in the visual cortex. On the other hand, animals raised with restricted pattern input (vertical or horizontal) usually develop squint, yet as shown by Blakemore & Cooper

(1970, 1971) have normal binocular activity in the visual cortex. Van Sluyters & Blakemore raised animals with artificial squint in vertical tubes similar to those used by Blakemore and Cooper. The result of this procedure was that even though the animals had squint, they developed normal binocularly active units. Thus, while cats with an artificial squint reared in a normal environment have few binocular units in the visual cortex, animals with squint raised in an environment consisting of a simple repetitive pattern have the normal number of cortical binocular cells.

These results can be interpreted as indicating that a basic requirement for the maintenance of binocular connections in the visual cortex of the cat is the simultaneous activation of corresponding retinal areas by similar stimuli. If the animal cannot align its visual axes, and if it is raised in the complexity of a normal environment, this requirement can never be met. On the other hand, if a similar animal is raised in an environment consisting of striped patterns, then although the same stimulus stripe cannot fall on corresponding areas of the two retinas, these areas will be stimulated in ways which are sufficiently similar to maintain binocular function.

The fact that animals raised in redundant environments develop squint suggests that although corresponding retinal points are probably specified at birth, the final alignment of the visual axes depends on specific visual input, probably during a critical period. In a normal visual field each area of the visual array is sufficiently different so that alignment of corresponding retinal points on unique visual elements will result in the normal alignment of the visual axes. It should be

pointed out that what is being suggested here is very similar in principle to what was suggested above for the development of orientation sensitive units in the visual cortex. Here too the developing visual system is seen as containing the rules of its own organization. With regard to the development of ocular alignment and binocular function it appears that a relatively simple set of rules can suffice. The eyes must be aligned in development so that each unique stimulus element falls on corresponding points of the two retinas. The results of the present work help to define the concept of a unique stimulus element. Animals raised in horizontal environments had the greatest degree of convergent squint, while animals raised in oblique environments had the least. Thus it can be concluded from the present results that stimuli organized along horizontal coordinates of the visual field are relatively unimportant in the process of initially aligning the visual axes.

Having considered the processes of the development of eye alignment and the development of binocular connections an attempt will now be made to consider in more detail the binocular interactions discussed previously. In the present work it was found that the receptive fields of binocularly active units were either located at corresponding points on the two retinas, or were shifted in their location in a direction and amplitude related to the degree of eye deviation. In one case both these arrangements were found in the same animal and since there is no reason for believing that this animal was unique it can probably be assumed that all animals reared with restricted pattern input have both normally corresponding and anomalously corresponding cortical units.

The origin of the anomalous correspondence found in the present

study is not clear. It would be consistent with the discrepancies cited above between the present data and previous data (Blakemore & Cooper, 1970, 1971) if the anomalous correspondences found here develop through interaction with the normal environment. The possible sequence of events which occurs in animals reared with restricted pattern input could be as follows:

1. Early stimulation confined to, for example, vertical stripes results in the stimulation of corresponding retinal points by different vertical lines in the environment, and hence these areas develop normal binocular function.
2. Since corresponding retinal points are not stimulated by the same line, the degree of alignment achieved by the animal is abnormal.
3. At the termination of restricted visual experience, the normal developmental programme operating on the abnormal environment has resulted in an animal whose eyes have become aligned to a completely redundant world which exists only in the laboratory. If single units are recorded in the animal at this point or before visual experience in a normal environment, the units would presumably be relatively normal with regard to binocularity and retinal correspondence.
4. With continued experience in a normal environment the visual system aligned to a redundant environment becomes modified, and anomalous retinal correspondence develops which provides the animal with a form of binocular vision.

The four stages outlined above are a hypothetical sequence of development which would account for the present results and would not be inconsistent with what is known about the visual system. Schlaer (1971) raised kittens with visual experience limited to prisms which introduced

a vertical disparity between the two eyes. The result was a shift in the expected direction in the vertical field disparities of cells recorded in the visual cortex of these kittens. Berlucchi (unpublished observations) produced squint in adult cats by sectioning the oculomotor nerves. He found that anomalous correspondence between field disparities of single units developed in the direction necessary to reduce the squint. The work of Spinelli et al. (1972) also demonstrated considerable modifiability of adult nervous connections. Animals with no binocular units at the end of restricted visual experience develop binocular units as a result of normal experience. Also consistent with the notion that the modifiability of neural connection in kittens demonstrated here continues into adulthood are some recent findings by Turkel (unpublished observations) which suggest that the number of binocular units in adult animals deprived of vision in one eye for periods up to two years is severely reduced. Clearly more research is needed in this area to determine if the developmental sequence outlined above does occur, and to what extent the neural modifiability seen in kittens continues into adulthood.

All animals deprived of normal early pattern input were found to have developed a distinct pendular nystagmus which differed in amplitude for different animals. It was most obviously present while animals were engaged in active searching, did not depend on patterned stimulation of one or both eyes, and the movements were generally conjugate. Finally, it was shown that although animals had abnormal fixation patterns, the saccadic latency of these animals was within the normal range. The latter finding suggests that the eye movement deficit is selective for

the system responsible for maintaining fixation and, at least grossly, does not effect the system responsible for shifting fixation.

The eye movement abnormalities found in the present experiment differ from those previously reported by Riesen (1961) who found that monkeys reared in the dark develop a jerk-type nystagmus which is characterized by rapid eye movements in one direction followed by a slow return, and which differs markedly from the pendular nystagmus observed here. The jerk-type nystagmus shown by Riesen probably is related to the nystagmus seen in blind humans (Ohm, 1950) in which the eyes dart rapidly about in an apparently random pattern of large amplitude saccades.

Pendular nystagmus of the type reported here does frequently occur in humans (Cogan, 1956, 1967) and a brief analysis of one of the situations in which it occurs may shed light on the results of the present study. Cogan classifies pendular nystagmus as a form of congenital nystagmus which he calls "sensory-defect nystagmus". He maintains that "absence of central vision is the rule in pendular nystagmus and is generally held to be the cause of the nystagmus". He further points out that pendular nystagmus usually develops if central vision is lost before the age of two; while if central vision is lost after the age of six, generally no abnormal eye movements develop. Cogan suggests that any defect of central vision, either optical or neural, during this critical period, will result in pendular nystagmus. Further, it is generally true that the greater the visual loss, the greater the excursions of the nystagmus. These considerations have led some workers to suggest that this form of pendular nystagmus arises as an attempt to compensate for a central scotoma (Cogan, 1956).

A recent experiment by Daroff et al. (1973) provides further insight into the mechanism of pendular nystagmus. These authors describe the case of a young woman with apparently congenital, pendular nystagmus. This patient had severe hyperopic astigmatism which resulted in clearest vision for objects oriented horizontally in her visual field. In addition, she had alternating exotropia and orthoptic examinations revealed an absence of central fusion and stereopsis, as well as anomalous retinal correspondence. This woman's nystagmus had a frequency of 5 Hz with an amplitude of 4° and was identical in pattern in the light or darkness, but stopped when she closed her eyes. The striking finding of Daroff et al. was that pendular nystagmus was completely suppressed when she viewed (monocularly or binocularly) a vertical line subtending a visual angle of approximately 30 min. arc. The suppression effect occurred only when the stimulus line was within 15° of vertical with respect to the axis of the patient's head. Daroff et al. interpret their finding in terms of the probable altered distribution of orientation responsive neurons in their astigmatic patient (Freeman, et al., 1972; Freeman & Thibos, 1973; Mitchell et al., 1973). An alternative explanation will be considered.

In the view described here, visual development may depend on a complex sequence of processes involving relatively simple "rules" of organization in interaction with a normal environment. Malfunction of a process at an early stage in the sequence may affect later stages not because of any abnormality at these stages, but because of the application of normal "rules of development" on a now abnormal substrate.

An example of how relatively minor early disruptions can result in major later disruptions comes from consideration of the possible

sequence of events in the patient studied by Daroff et al. In considering this case the stages of development will be treated as if they were sequential though in fact much development must occur in parallel with complex feedback and feedforward mechanisms between developmental sequences. One could postulate that severe astigmatism was the initial defect in this patient. Her astigmatism allowed her to see clearly only lines oriented horizontally in her visual field, and, as shown in the present study, early input restricted to horizontal stimuli is not sufficient to develop normal eye alignment. A squint developed, and since normal retinal correspondence could not be maintained she developed anomalous correspondence. It can be seen how this patient is very similar to the animals studied here which also develop squint and anomalous correspondence following restricted early input. In addition, the animals studied here also developed pendular nystagmus as did this patient.

It seems at least possible that pendular nystagmus is related most closely not to the astigmatism of this patient, but rather to her anomalous correspondence. Due to her anomalous correspondence each retinal representation contains two separate areas corresponding to a single visual direction: the "innate" corresponding area, and the anomalous corresponding area. Pendular nystagmus can perhaps be seen as the shifting back and forth between corresponding areas. The results of Daroff et al. can be interpreted as indicating that the shift depends on simultaneous vertical stimulus input on both corresponding areas. In a simplified environment where only a single vertical stimulus is present the shift ceases.

Some results of the present experiment are consistent with the

notion that pendular nystagmus is related to anomalous correspondence. If this relation exists and the degree of anomalous correspondence is related to the degree of eye deviation as shown in the present study, then the amplitude of pendular nystagmus should be directly related to the degree of eye deviation. This was, approximately, the case in the present study, with the animals reared with horizontal visual experience displaying larger amplitude pendular nystagmus than the animals reared with oblique visual experience. An additional result that should follow from the relation of pendular nystagmus to anomalous correspondence is that if anomalous correspondence depends on experience in a normal environment, so should pendular nystagmus. This too was found to be roughly the case in the present study, with nystagmus becoming more evident some months after restricted rearing that immediately after the period of restriction. In addition, Cogan (1966) points out that in humans pendular nystagmus is rarely apparent until several weeks after birth.

The eye movement abnormalities observed in the present study may be seen then in the context of the total developing organism. If the analysis of these abnormalities described above is correct then these abnormal eye movements shed light, not so much on the normal pattern of eye movement development, but rather on the kind of interaction that can occur between developing systems. The observations on normal development reported here suggest that the eye alignment system and the eye movement system develop roughly in parallel with the development of visual function. The effects of specific early input on these systems highlight the complex interactions which occur during development and shed some light on the

specific requirements of normal development.

In the present study the organism has been viewed as a kind of machine which has the peculiar ability to create itself. The possibility has been explored that a limited number of relatively simple rules can suffice for transforming environmental patterns into patterns in the nervous system. An attempt has been made to outline some rules governing one small part of this continuing transformation.

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Appendix

Optic Disc Separation in Paralyzed State

Cat	Distance from rear projection screen (cm.)	Distance between optic disc centers (cm.)	Tangent	Visual angle (degrees)
H-1	42	9.8	.234	13.2
H-2	41	12	.293	16.3
V-2	43	20.5	.477	25.5
V-1B	42	18	.429	23.2
V-2B	43	20	.465	24.9
O-1	43	26	.605	31.2
O-2	42	21.5	.512	27.1
O-1B	42	23.2	.552	28.9
O-2B	42	21.5	.512	27.1
Da-1	43	21.5	.500	26.6
Di-1	42	19.5	.465	24.9
UNRC	42	22.5	.536	28.2
RC-1	43	27	.628	32.1
RC-2	42	23.7	.564	29.4
A03	43	26	.605	31.2
A01	45	26.5	.589	30.5

Summary of Single Cell Data

Cat	# of penetrations	# of units encountered		# of clusters encountered		Fibres		No Following			
		bin-ocular	IPS	Cont.	ocular	IPS	Cont.	units	clusters	units	clusters
H-1	4	2	1	1	1	1	1	-	1	-	-
H-2	6	3	3	3	4	-	2	-	-	2	-
V-2	5	2	2	1	2	-	1	2	-	2	-
V-1B	5	4	3	5	6	-	1	1	-	2	-
V-2B	4	-	1	1	-	-	1	-	-	-	-
O-1	4	2	4	6	4	-	1	2	3	4	-
O-2	5	3	3	2	6	1	2	2	1	2	-
O-1B	3	-	-	3	4	1	4	-	2	-	-
O-2B	3	-	-	7	1	-	1	-	-	-	-
Dar-1	4	2	1	2	2	2	2	1	1	6	1
DI-1	5	5	-	2	4	-	1	1	1	3	1
UNRC	7	7	1	4	8	1	-	-	-	-	-